

GEOMORPHIC AND HYDROLOGIC FACTORS INFLUENCING
THE DISTRIBUTION OF RIVER SHOALS AND ASSOCIATED BIOTA

by

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(Under the direction of Judith L. Meyer)

ABSTRACT

Understanding the geomorphic and hydrologic relationships to instream flora and fauna is essential to successful management of stream and river environments. Broadly, this dissertation research addresses these relationships by investigating hydrologic and geomorphic factors that control imperiled fish habitats in the Etowah River, Georgia. Specifically, I examined factors affecting shoal (i.e., shallow parts of river channels) sediment composition and *Podostemum ceratophyllum* (riverweed; an aquatic macrophyte).

Channel incision caused by channelization or altered hydrology typically reduces habitat complexity and alters sediment composition. Sediment composition and *P. ceratophyllum* did not differ between incised and slightly incised shoals. Measurements following a flood indicated that bed mobility affects *P. ceratophyllum* occurrence and length (a correlate of biomass), and may have a stronger effect than channel incision. Proportion bedrock and channel width accounted for 77% of the variation in *P. ceratophyllum* occurrence among sites, while proportion cobble and basin area accounted for 51% of *P. ceratophyllum* length variance. Shade, water velocity, and sediment size cumulatively accounted for 47% of the variance in *P. ceratophyllum* density, 32% in length, and 22% in biomass within sites.

Based on the Network Dynamics Hypothesis (NDH), I predicted that tributaries influence mainstem morphology via tributary sediment inputs and that alluvial shoals occur below large tributary confluences. Although tributary basin area and the ratio of tributary to mainstem basin area did not predict shoal occurrence, alluvial shoals were closer to upstream confluences than were other shoal types, indicating an association with tributaries. Shoals near large tributary confluences also contained a larger proportion of gravel and cobble bed sediments and were wider than adjacent, downstream shoals. These geomorphic differences are likely to affect *P. ceratophyllum* occurrence and length.

Monthly and annual monitoring indicated that *P. ceratophyllum* biomass was highest in late summer and lowest during winter and periods of low stream flow. Among years, *P. ceratophyllum* presence and length increased as discharge decreased. Precipitation changes and management actions that affect river flows are likely to affect macrophyte occurrence and associated fauna.

Cumulatively, these results suggest that landscape or shoal-scale restoration approaches that increase the proportion of coarse sediment in shoals are likely to increase *P. ceratophyllum* occurrence, length, and persistence.

INDEX WORDS: *Brachycentrus etowahensis*, Entrenchment ratio, Etowah caddisfly, Etowah River, Georgia, Incision, Network dynamics hypothesis, *Podostemum ceratophyllum*, Riverweed, Rosgen Classification of Natural Rivers, Sediment, Shoal, Stream flow

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TABLE OF CONTENTS

CHAPTER	PAGE
1. INTRODUCTION.....	1
2. DOES GEOMORPHIC DEGRADATION PREDICT INSTREAM HABITAT DEGRADATION? EXAMINING IMPERILED FISH HABITAT DIFFERENCES ALONG A CHANNEL INCISION GRADIENT.....	9
3. GEOMORPHIC FACTORS INFLUENCE THE DISTRIBUTION OF A DOMINANT AQUATIC MACROPHYTE AND AN ENDEMIC CADDISFLY IN A SOUTHEASTERN RIVER.....	36
4. LARGE CHANNEL CONFLUENCES INFLUENCE GEOMORPHIC HETEROGENEITY OF A SOUTHEASTERN RIVER.....	59
5. THE INFLUENCE OF INTERANNUAL FLOW VARIABILITY ON A SOUTHEASTERN AQUATIC MACROPHYTE.....	82
6. CONCLUSION.....	111
APPENDIX.....	116

CHAPTER 1

INTRODUCTION

Aquatic ecosystems are highly sensitive to anthropogenic disturbances. Land use change can increase fine sediment inputs to streams, degrade water quality, and impact native flora, fauna, and ecosystem function (Paul and Meyer 2001, Allan 2004). Consequently, aquatic communities of today are often legacies of past land use (Harding et al. 1998), and present land use change and population growth continues to impact stream habitats while placing greater demands on water supply. Cumulatively, both historic and current impacts have contributed to the imperilment of over half of fish (Walsh et al. 1995) and mussel (Williams and Neves 1995) species in the southeastern United States. As the awareness of species imperilment and the importance of aquatic ecosystem services grow, so does interest in restoring streams and their habitats.

Hence, understanding the geomorphic and hydrologic relationships to instream flora and fauna is essential to successful management of stream and river environments. Broadly, this dissertation research addresses these relationships by investigating hydrologic and geomorphic factors that control important instream habitat features (Figure 1.1).

My dissertation research focuses on shoals in the Etowah River, Georgia. Shoals are shallow parts of river channels (USDA 2003), generally with higher gradients than surrounding channel units. Shoals in the Etowah River above Lake Allatoona are biologically diverse, harboring both state and federally listed species such as the Etowah darter (*Etheostoma etowahae*), amber darter (*Percina antesella*), freckled darter (*Percina lenticula*), “Coosa” madtom (*Noturus* sp. cf. *N. munitus*), and endemic Etowah caddisfly (*Brachycentrus etowahensis*). The occurrence of

several imperiled fishes increases in the presence of *Podostemum ceratophyllum* (Freeman et al. 2003, Hagler 2006, Argentina 2006), an aquatic macrophyte that grows on rocky shoals. The high species diversity, large number of imperiled species, and presence of ecologically important shoal habitats make the Etowah River an important location to assess the effects of geomorphic variation on instream habitats.

Among the instream habitat variables that are relevant to imperiled species in the Etowah River, one of the most important is riverweed (*Podostemum ceratophyllum*, Michx; Freeman et al. 2003, Hagler 2006), an aquatic macrophyte. However, the distribution of this macrophyte varies tremendously among shoals in the Etowah River. Understanding causes of this variation can improve detection and prediction of patterns of macrophyte distributions, the species with which they are associated, and ultimately help guide future restoration efforts.

Channel geomorphology likely affects *P. ceratophyllum* distributions. Channel incision caused by channelization or altered hydrology reduces habitat complexity and alters sediment composition (Darby and Simon 1999, Davies et al. 2005). Because coarse, stable sediments in shoals contribute to the proliferation of *P. ceratophyllum* in Piedmont streams (Nelson and Scott 1962, Argentina 2006), and because incision affects sediment dynamics, geomorphically degraded, incised shoals also may have reduced *P. ceratophyllum* occurrence. Additionally, water depth influences the degree of light penetration to bed sediments, and influences primary production. Wide shoals probably have less shade than narrow shoals, potentially resulting in increased *P. ceratophyllum* occurrence and productivity. Thus, multiple geomorphic factors may control *P. ceratophyllum* distribution and my research tests for these relationships (Figure 1.1). Chapter 2 examines the relationship between geomorphic degradation and habitat quality by assessing the relationships between the degree of channel incision, *P. ceratophyllum*, and

sediment composition. It also examines the effects of floods and geomorphology on *P. ceratophyllum* occurrence and length. Chapter 3 examines the relationships among geomorphic variables, *P. ceratophyllum* and caddisflies among a larger diversity of shoal types and throughout a larger segment of the Etowah River.

Although *P. ceratophyllum* predominantly occurs in rocky shoals, shoals themselves vary widely in their sediment composition and channel dimensions. Because variations in sediment composition influence the distribution of imperiled fishes (Freeman et al. 2003) and macrophytes (Chapter 2), understanding the processes that affect sediment size and channel form variation are of interest to both scientists and managers. In other river systems, bed texture fining is punctuated by particle size increases near confluences (Church and Kellerhals 1978, Knighton 1998, Troutman 1980). Tributary sediment inputs can increase channel slope and shear stress below tributaries (Rice et al. 2001). Discharge increases at confluences can cause channels to widen, thereby increasing light penetration to the streambed and primary and secondary productivity (Rice et al. 2001). However, the potential of a tributary to influence mainstem morphology increases with tributary basin area in western drainages (Benda et al. 2004). These relationships have largely gone untested in eastern streams and rivers, but I hypothesize that a considerable amount of geomorphic variation exists in part due to lateral sediment inputs at tributary junctions. Thus, Chapter 4 examines the effects of tributary basin area and sediment composition on the geomorphology and distribution of shoals in the Etowah River, Georgia (Figure 1.1).

Chapters 2-4 examine hydrological, geomorphological, and ecological relationships among and within shoals. There also can be considerable interannual habitat variation induced by both natural (Poff et al. 1997) and anthropogenic hydrologic changes (Richter et al. 1997).

Climate change, increased water allocation for consumptive, and flow regulation use have placed increased demands on freshwater streams and rivers (Palmer et al. 2008), and such changes are likely to alter stream flows. On a global scale, both evaporation and precipitation are expected to increase (Li et al. 2007). Although climate predictions for precipitation in the southeastern U.S. are less certain (Hengeveld 2000, IPCC 2007), some models forecast decreases in precipitation (Hengeveld 2000) with likely consequences for stream flow. These predicted changes make understanding ecologically important macrophyte responses to interannual flow variation a high priority.

We anticipate that *P. ceratophyllum* is extremely responsive to flow variability and associated water quality changes, even in the absence of complete stream dewatering or large floods. For example, during drought, water temperature generally increases as flow decreases (Cowx et al. 1984), potentially affecting plant physiology, distribution, and nutrient uptake (Lambers et al. 1998). In the absence of wastewater effluent inputs, dry periods also may be characterized by lower stream nutrient levels because of reduced runoff (Caruso 2002) and increased groundwater contribution to stream flow (Dahm et al. 2003), potentially affecting plant growth (Cushing and Allan 2001, Hillebrand 2002). Given the important ecological roles of aquatic macrophytes and their potential susceptibility to water quality and quantity changes, we may expect substantial ecological consequences should flow-induced changes in plant growth occur. Thus, Chapter 5 examines the effects of river flow and precipitation on interannual variation in *P. ceratophyllum* presence and morphology (Figure 1.1).

Collectively, these chapters address our understanding of the hydrological and geomorphological factors that control ecologically important instream habitats. They also

identify important knowledge gaps and attempt to address them in a manner that not only contributes to management, but also to enhancing scientific understanding of aquatic ecosystems.

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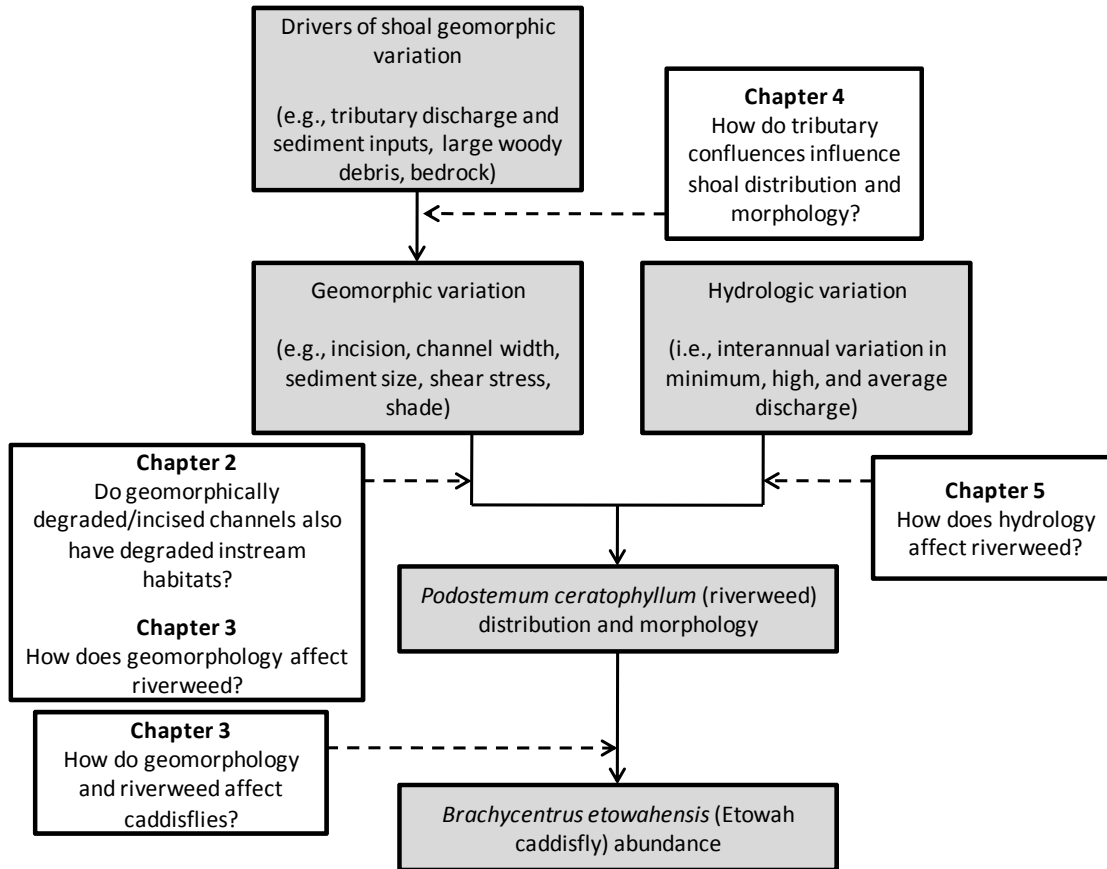


Figure 1.1. Relationship of dissertation research (white boxes, dashed arrows) to hypothesized relationships (solid arrows) of factors that influence shoal geomorphic variation, *Podostemum ceratophyllum*, and *Brachycentrus etowahensis*.

CHAPTER 2

DOES GEOMORPHIC DEGRADATION PREDICT INSTREAM HABITAT DEGRADATION? EXAMINING IMPERILED FISH HABITAT DIFFERENCES ALONG A CHANNEL INCISION GRADIENT

¹W.W. Duncan and J.L. Meyer. Submitted to *Restoration Ecology*.

ABSTRACT

Incised channels are dynamic components of fluvial systems, represent geomorphically degraded stream and river channels, and are encountered worldwide. The ecological effects of channel incision can be far-reaching, affecting habitat complexity, habitat availability, aquatic and terrestrial flora and fauna and channel processes. Although channel incision represents geomorphic degradation and can reflect habitat degradation, some studies suggest that important instream habitats do not differ with the degree of incision. Therefore, we tested whether instream habitat variables that are important to imperiled fishes differ in river reaches with varying degrees of incision.

Using entrenchment ratio as a measure of incision, incision had no discernable effect on habitat characteristics. However, principal components representing other geomorphic variables (e.g., bank height, bed mobility, D_{84} , cross-sectional area, bankfull width, and wetted perimeter) accounted for as much as 75 % of macrophyte occurrence and 64 % of length variance.

Additional surveys following a flood indicated that macrophyte occurrence on cobble declined as bank height and bed mobility increased, and sediment size decreased. Combined, these results suggest that sediment size and bed mobility have a stronger influence on instream habitat than the influence of channel incision.

Although incision is a sign of geomorphic degradation, important aspects of instream habitat are not described by this geomorphic measurement. Restoration strategies that depend on incision to identify restoration sites may have limited instream habitat benefits in Southeastern Piedmont streams and rivers. Instead, landscape or shoal-scale restoration approaches that increase the proportion of coarse sediment may increase macrophyte occurrence, length, and persistence.

INTRODUCTION

Incised channels are dynamic components of fluvial systems and are encountered worldwide. By definition, incised channels have experienced bed-level lowering, or degradation, often as a consequence of channelization or increased flow energy and sediment transport capacity relative to sediment supply (Lane 1954). Consequently, channel incision may arise from natural phenomenon (e.g., base level lowering or meander cutoff) or human actions (e.g., channelization, urbanization, dam construction) that interrupt naturally dynamic flow or sediment regimes. Streams and rivers that have incised are also referred to as entrenched (Schumm 1999), and both terms are used interchangeably to describe geomorphic degradation associated with bed-level lowering.

Channel bank erosion, bridge undermining, water table lowering, and increased sediment export are among the many environmental and societal impacts associated with channel incision (Bravard et al. 1999). The ecological effects of channel incision are far-reaching. Water table lowering reduces groundwater storage and may cause mortality of riparian vegetation (Reilly and Johnson 1982). Incision can cause channel simplification, reducing habitat complexity (Davies et al. 2005), channel margin habitats, and impacting fish communities (Shields et al. 1994). Consequently, incised or incising channels are often targeted for restoration or rehabilitation with the goal of improving degraded habitats or preserving unaffected stream reaches (Bravard et al. 1999, Rosgen 1997, Shields et al. 1999).

Although incision is an indicator of geomorphic degradation and can reflect habitat quality, some evidence suggests that incision may not reflect habitat degradation. Sediment size, gradient, and important coldwater fish habitats did not differ among Idaho streams with varying degree of incision (Kappesser 2002). Conversely, considerable instream habitat and geomorphic

variation may exist within entrenchment classes (*sensu* Rosgen 1996). Riffle stability, residual pool volume, and fish habitat measurements varied considerably within incised and moderately incised streams, depending on watershed timber management (Cross and Everest 1995, Kappesser 2002). Consequently, these studies suggest that channel entrenchment or incision may not reflect watershed disturbances or instream habitat degradation.

We tested whether channel incision reflects instream habitat quality by comparing instream habitat variables relevant to imperiled fishes in river reaches with varying degrees of incision. We also assessed other geomorphic variables as predictors of instream fish habitat, and we propose and test a potential mechanism by which these predictors influence habitat; namely that particle stability facilitates the persistence of aquatic macrophytes during floods.

Study System

This research was conducted in shoals of the upper Etowah River (34° 21' N, 84° 06' W), a north Georgia U.S.A. river that drains the Southern Blue Ridge and Piedmont physiographic provinces. Shoals are shallow parts of river channels (USDA 2003), generally with higher gradients than surrounding channel units. Causes of channel incision at all shoals are unknown, but incision may be a consequence of historic, intensive agricultural practices that altered hydrology and increased sediment transport capacity. Although a thorough examination of historic channelization was not conducted throughout the study area, satellite imagery and field observations indicated that one site on the Etowah River showed evidence of channelization, potentially resulting in widespread channel incision.

Shoals in the Etowah River above Lake Allatoona are biologically diverse, harboring both state and federally listed species such as the Etowah darter (*Etheostoma etowahae*), amber darter

(*Percina antesella*), freckled darter (*Percina lenticula*), “Coosa” madtom (*Noturus* sp. cf. *N. munitus*), and endemic Etowah caddisfly (*Brachycentrus etowahensis*). Given the biological relevance of Etowah River shoals, understanding the relationship between geomorphic degradation and habitat degradation is of interest to scientists and managers.

The “Coosa” madtom, freckled darter, and Etowah darter commonly are found over cobble and gravel sediments (Suttkus and Taylor 1965; Suttkus and Ramsey 1967; Wood and Mayden 1993; USFWS 1993; USFWS 1994; Freeman et al. 2003). Fine sediment accumulation is a stressor to these fishes (Wenger and Freeman 2006). Thus, coarse and fine sediment are habitat variables of interest to managers because of their relevance to imperiled fishes.

In the Etowah River, the madtom and darters are significantly more likely to occur in the presence of riverweed, *Podostemum ceratophyllum* (riverweed) Michx. (Freeman et al. 2003; Hagler 2006), a rheophyllic macrophyte that grows in shoals. *P. ceratophyllum* increases surface area of the stream bed 3-4 times over bare rock (Hutchens et al. 2004) thereby facilitating high total macroinvertebrate biomass and abundance (Grubaugh and Wallace 1995; Grubaugh et al. 1997), including the endemic Etowah caddisfly (Willats 1998). Given the importance of this plant in shoal ecosystems, it too is an important habitat variable.

METHODS

Etowah River shoal surveys were initiated from late July – early September, 2004, and again from late October – early November after a flood associated with Hurricane Ivan (September 17, 2004) overtopped riverbanks at all sites. The river above Yellow Creek Road and below State Route 136 (48 km) was selected as the study reach because it is designated as high priority for restoration and preservation by USFWS (Freeman and Wenger 2000), is of relatively uniform gradient, and is dominated by alluvial processes. Fifteen sites were chosen based on

accessibility, but all were dispersed throughout the river segment by selecting sites above and below third order tributaries.

The downstream shoal boundary was determined at base flow as the location at which water depth exceeded 0.6 m, which is the point at which thalweg depth significantly increased in our preliminary shoal investigations. Thus, the upstream extent of shoals was also selected at a water depth of 0.6 m.

Sites were classified as incised, moderately incised, or slightly incised using the entrenchment ratio method outlined in Rosgen (1996). This method was chosen because it is widely used by scientists and managers to assess channel incision throughout the United States. To calculate entrenchment ratio, a cross section at mid-shoal was made generally following methods outlined in Harrelson et al. (1994). Bankfull elevation was identified by two individuals, one of which was trained in Rosgen restoration classes. The entrenchment ratio was calculated as the width of the flood prone area measured at twice maximum bankfull depth, divided by bankfull channel width (Table 2.1, Rosgen 1996). Sites were divided into entrenchment ratio categories (<1.4 for incised; 1.4-2.2 for moderately incised; and >2.2 for slightly incised; Rosgen 1996).

Width to depth ratio (W:D) was also calculated using bankfull measurements and the channel cross sections, as it is often used as a descriptor of channel dimensions and may account for variation in habitat measurements (Table 2.1, Rosgen 1996).

Wolman pebble counts were used to measure sediment size of a minimum of 100 sediments per shoal (Wolman 1954). Counts were conducted along 10-12 transects equidistantly spaced to span the entire shoal length. To characterize instream habitat, bank sediments were not included

in the pebble count. Habitat variables derived from the pebble counts for each site included the proportion of fines (≤ 2 mm), gravel (2-63 mm), and cobble (64-255 mm).

Each particle collected in the pebble count was visually assessed for the presence of *P. ceratophyllum*. Because of the large number of plant stems on a particle and the impracticality of measuring multiple stems or biomass, maximum plant length was recorded. Maximum length provided a standardized plant quality measurement repeatable among observers. Thus, instream habitat variables for each site included the average *P. ceratophyllum* length measurements and *P. ceratophyllum* frequency of occurrence (calculated as the proportion of all particles with *P. ceratophyllum* present).

Statistical Analysis

Comparison of incised, moderately incised, and slightly incised channels.

To test whether incision categories in the Rosgen Classification of Natural Rivers had significantly different instream habitat characteristics, sites were divided into entrenchment ratio categories (8 entrenched/incised sites, 0 moderately incised sites, and 7 slightly incised sites, Rosgen 1996). Student's t-test was used to test for habitat differences between incised and slightly incised sites, and an a priori p-value of 0.10 was selected as the threshold for statistical significance. A retrospective power analysis was used to determine the sample size necessary to detect statistical significance at $\alpha = 0.10$ and power = 0.80.

Assessment of alternative geomorphic predictors

A subsequent analysis, using variables derived from the sediment and channel geometry measurements described above, assessed whether channel geometry (11 variables), sediment transport (6 variables), or sediment size (12 variables) were predictors of instream habitat (Table

2.1). Variables with correlation coefficients greater than 0.40 with *P. ceratophyllum* occurrence or length (Table 1) were selected as potentially important instream habitat predictors. The sediment size variable with the highest correlation coefficient with length and occurrence was chosen to represent sediment size. Because some predictor variables were correlated, axes from Principal Components Analyses with eigenvectors greater than 1 were used to represent predictor variables in regression analyses described below. Principal components were calculated in PC-ORD (McCune and Mefford 1999).

Post-flood *P. ceratophyllum* assessment.

To test whether *P. ceratophyllum* occurrence or length changed following a flood event, and whether the amount of change depended upon particle size, pebble counts and *P. ceratophyllum* measurements were repeated after a hurricane-generated flood at 9 shoals using upstream and downstream boundaries from the previous survey. Data were grouped into gravel, cobble, and boulder/bedrock classes and analyzed using repeated measures ANOVA. Proportion of fines was omitted from the analysis because *P. ceratophyllum* is rarely found on sediments less than 2 mm. To compare the likelihood of *P. ceratophyllum* loss among sediment classes, the ratio of post- to pre-flood occurrence and length was compared among classes using an ANOVA.

A second analysis tested whether change in *P. ceratophyllum* varied along the principal component axes identified earlier. Pre- and post-flood *P. ceratophyllum* occurrence and length differences were calculated for each sediment class for each site. Analysis of covariance was used to assess whether the effects of sediment size (a class variable) on *P. ceratophyllum* differences depended upon principal components (i.e., the covariates). Significant class*covariate interactions indicate that covariate effects depend on class (Sokal and Rohlf

1995). An a priori p-value of 0.10 was selected as the threshold for statistical significance on all tests. Analyses were conducted using SAS version 8 (SAS Institute, Cary, NC).

RESULTS

Comparison of incised, moderately incised, and slightly incised channels.

Incised and slightly incised channels were identical for habitat variables measured (Figure 2.1, Appendix A). All sites had high W:D ratios ($W:D > 12$). There was no difference between incised sites and slightly incised sites for *P. ceratophyllum* occurrence ($t = 0.45$, $df = 13$, $p = 0.66$), *P. ceratophyllum* length ($t = 1.05$, $df = 6.93$, $p = 0.33$, using Satterthwaite method recommended for unequal variances), proportion fines ($t = -0.38$, $df = 13$, $p = 0.71$), proportion gravel ($t = -0.99$, $df = 13$, $p = 0.34$), and proportion cobble ($t = 0.92$, $df = 13$, $p = 0.38$). Sample sizes necessary to detect statistical significance for each habitat variable are extremely large (Table 2.2).

Assessment of alternative geomorphic predictors

Correlation matrices indicated that bank height, bed mobility, and D_{84} were correlated with *P. ceratophyllum* occurrence among sites (Table 2.1). Principal Components Analysis using these three variables indicated that the first principal component (Occurrence Principal Component 1) was correlated positively with bank height, bed mobility, and negatively with D_{84} (Table 2.1). This axis accounted for 75 % of the variation in *P. ceratophyllum* occurrence (Figure 2.2: $F_{[1,13]} = 39.4$, $p < 0.0001$) among shoals.

P. ceratophyllum length was positively correlated with cross-sectional area, bankfull width, wetted perimeter, and D_{84} , and negatively correlated with bank height (Table 2.1). Principal Components Analysis indicated that the first axis (Length Principal Component 1) was

negatively correlated with cross-sectional area bankfull width and wetted perimeter, while the second axis (Length Principal Component 2) was correlated negatively with bank height and positively with D_{84} (Table 1). Stepwise multiple regression analysis indicated that both axes cumulatively accounted for 64% of the variance in *P. ceratophyllum* length among shoals (Figure 2.3: $F_{[2,12]} = 10.59$, $p = 0.002$).

Post-flood *P. ceratophyllum* assessment

Both before and after Hurricane Ivan, *P. ceratophyllum* occurrence increased as sediment size class increased (Figure 2.4a: $F_{[2,19]} = 7.6$, $p = 0.004$). *P. ceratophyllum* occurrence was lower after the flood on all sediment classes (Figure 2.4a: $F_{[1,19]} = 14.1$, $p = 0.001$). The decrease in *P. ceratophyllum* occurrence over time did not vary among sediment classes (Figure 2.4a: sediment class*time: $F_{[2,19]} = 0.48$, $p = 0.48$) and the likelihood of a decline in *P. ceratophyllum* occurrence did not vary among sediment classes ($F_{[2,21]} = 2.0$, $p = 0.16$; results not shown).

P. ceratophyllum length decreased (Figure 2.4b: $F_{[1,19]} = 10.8$, $p = 0.004$) following Hurricane Ivan, but *P. ceratophyllum* length did not differ among classes (Figure 2.4b: $F_{[2,19]} = 2.2$, $p = 0.14$). There was no sediment size class by time interaction (Figure 2.4b: $F_{[2,19]} = 0.11$, $p = 0.90$), indicating that length change did not depend on sediment class. The likelihood of a decline in *P. ceratophyllum* length did not vary among sediment classes ($F_{[2,21]} = 0.4$, $p = 0.66$; results not shown).

Analysis of covariance on pre- and post-flood *P. ceratophyllum* occurrence differences indicated a significant interaction between Occurrence Principal Component 1 and sediment size class (Figure 2.5: sediment class $F_{[1,13]} = 0.00$, $p = 0.95$; PC1 $F_{[1,13]} = 2.01$, $p = 0.17$; PC1*sediment class: $F_{[1,13]} = 3.89$, $p = 0.07$). Occurrence differences on cobble increased as shoal bank height and bed mobility increased, and as D_{84} decreased (Figure 2.5). Occurrence

differences on gravel were uniform along the principal component 1 gradient. ANCOVA on pre- and post-flood *P. ceratophyllum* length differences indicated no significant effect of principal components, sediment size class or interactions (data not shown; $p > 0.10$).

DISCUSSION

Instream habitat variables that are important to imperiled Etowah River fish include the proportion of fines, cobble, and gravel in sediments and the presence of *P. ceratophyllum* (Suttkus and Taylor 1965; Suttkus and Ramsey 1967; Wood and Mayden 1993; U.S.FWS 1993; Freeman 1999; Freeman et al. 2003; Wenger and Freeman 2006; Hagler 2006). However, these variables did not differ between incised and slightly incised sites. Furthermore, retrospective power analyses indicated that sample sizes greater than the 87 shoals present in this river segment would be necessary to detect statistically significant habitat differences for most habitat variables (Table 2.1). Thus, it is unlikely that biologically meaningful habitat differences between incised and slightly incised sites can be detected in the Etowah River.

There are several potential explanations for the lack of instream habitat differences between geomorphically degraded incised sites and less-degraded slightly incised sites. First, entrenchment ratio was used to quantify incision, and was measured as the ratio of flood prone area width (measured at twice maximum bankfull depth) to bankfull width ($W_{fpa}:W_{bkfl}$; Rosgen 1996). Thus, streams in naturally narrow valleys with small flood prone areas can be classified as incised. Valley width was wider than the W_{fpa} at all incised shoals, and therefore does not account for the lack of a relationship between incision and habitat quality in this river.

The lack of imperiled species habitat differences between incised and slightly incised sites is particularly interesting in the context of channel restoration for habitat improvement purposes.

Incision is often used in combination with additional variables (e.g., species distribution data) to select restoration sites (Rosgen 1997). But our results suggest that important instream habitat variables did not differ between incised and slightly incised sites and that entrenchment ratio should be used cautiously when selecting restoration sites.

Although incision is a sign of geomorphic degradation, important aspects of instream habitat are not described by this geomorphic measurement. Stream habitats and fauna are a reflection of upstream (Frissell et al. 1986; Sutherland et al. 2002; Roy et al. 2003; Walters et al. 2003a; Walters et al. 2003b) and historic (Harding et al. 1998; Scott and Helfman 2001) watershed characteristics as well as local influences (Frissell et al. 1986; Pringle et al. 1988; Walters et al. 2003b; Roy et al. 2007). Thus, processes contributing to channel incision (i.e., altered sediment and/or flow regimes stemming from historic intensive agricultural land use and channelization) occurred at spatial and temporal scales that are not the most relevant to present-day imperiled instream habitat for fish. The effects of historic geomorphic degradation were not manifested in the habitat metrics used in this study.

Bank height, bed mobility, D_{84} , bankfull width, and wetted perimeter were implicated as important predictors of *P. ceratophyllum* occurrence and length. We hypothesized a potential mechanism, namely that particle stability facilitates the persistence of these rheophilic plants. Particle stability is a function of the channel dimensions (increasing with channel width and decreasing as flows are confined by tall banks) and sediment size (increasing with D_{84}). The Hurricane Ivan flood afforded us an opportunity to test this hypothesis.

While occurrence and length decreased following the flood, the absolute decrease and the likelihood of decrease were the same among sediment classes. However, regressions with principal components indicate that on cobble, *P. ceratophyllum* occurrence and length declined

as bank height and bed mobility increased, and occurrence declined as shoal D_{84} decreased. In other words, there was a greater decline in *P. ceratophyllum* occurrence and length after the storm in shoals with fewer large particles and where a greater proportion of the bed was mobilized. Contrary to our expectations, *P. ceratophyllum* occurrence on gravel showed no change along the same axis. One explanation is that the flood was of sufficient magnitude to affect *P. ceratophyllum* on gravel similarly among sites, regardless of shoal channel dimensions or D_{84} . Indeed, nearly 100% of all gravels among sites were mobilized (proportion from the bed mobility calculations: $\bar{X} = 0.99 \pm 0.004$) during the flood in contrast to the variable proportion of cobbles mobilized among sites ($\bar{X} = 0.59 \pm 0.14$). Thus, it is likely that *P. ceratophyllum* on gravels was buried or exported at all shoals, whereas the decline in *P. ceratophyllum* on cobble was more variable among sites because not all cobbles were mobilized at all sites.

CONCLUSION

Although incision is a sign of geomorphic degradation, instream habitat variables relevant to imperiled fishes did not differ between incised and slightly incised sites. This suggests that incision should be used cautiously when inferring habitat quality and identifying restoration sites for habitat improvement. The observation that floods, channel geometry, and sediment size are useful predictors of *P. ceratophyllum* occurrence and length illustrates the importance of shoal-scale geomorphology to instream habitat, with sediment size playing a principal role.

Restoration approaches that increase instream sediment size may increase *P. ceratophyllum* occurrence, length, and persistence. Restoration strategies that restore the natural processes that form and maintain shoals (e.g., coarse and fine sediment origin, hydrologic regimes that promote coarse sediment transport throughout a river network, and deposition into shoals), may also be

successful in the long-term management of imperiled species habitats. Sediment budgets are useful in this regard, enabling managers to determine the magnitude of sediment delivery from tributaries, channel banks, and upland sources, and empowering them to strategically target restoration efforts.

IMPLICATIONS FOR PRACTICE

- Geomorphic degradation doesn't necessarily equate to habitat degradation: incised and slightly incised sites did not differ in their proportions of endangered fish instream habitat.
- Entrenchment ratio should be used cautiously when selecting a restoration site or inferring habitat quality.
- Stream bed mobility, sediment size (D_{84}) and bank height are better geomorphic predictors of *P. ceratophyllum* in the Etowah River.
- In the Etowah River, and likely beyond, restoration approaches that incorporate geomorphological-ecological linkages are more likely to be successful than those that rely on incision.

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Table 2.1. Variable definitions and Pearson's correlation coefficients of predictor variables and *P. ceratophyllum* occurrence, length, and their respective principal components. Only coefficients with occurrence and length that are > 0.40 are shown.

	<i>P. ceratophyllum</i> occurrence	Occurrence PC1	<i>P. ceratophyllum</i> length	Length PC1	Length PC2
Channel Geometry					
<i>Slope (S)</i> - change in elevation from the top to bottom of the shoal, divided by the shoal length.					
<i>Cross-sectional area (A)</i> - area of the channel cross-section at bankfull elevation.			0.55	-0.95	
<i>Width at bankfull (Wbkfl)</i> - width of river channel at bankfull stage.			0.47	-0.97	
<i>Maximum depth at bankfull</i> - maximum distance from river bed to water surface at bankfull stage.					
<i>Bank height</i> - height of the lowest bank relative to the river bed.	-0.46	0.71	-0.42	-0.36	-0.87
<i>Mean depth</i> - mean depth of channel at bankfull stage. Calculated from cross-sectional area divided by width at bankfull.					
<i>Wetted perimeter</i> - length of the bed and banks along the channel cross-section.			0.48	-0.98	
<i>Hydraulic radius (R)</i> - cross-sectional area divided by wetted perimeter.					
<i>Width : depth ratio</i> - bankfull width divided by the mean bankfull depth.					
<i>Shoal length</i> - distance from top to bottom of shoal. Top and bottom of shoals was determined at a depth of 0.6 cm as described in methods.					
<i>Entrenchment ratio (Wfpa/Wbkfl)</i> - flood prone area width (Wfpa) divided by bankfull width. Flood prone width is determined at an elevation twice the maximum depth at bankfull.					
Sediment Transport					
<i>Shear stress</i> - force exerted on riverbed during bankfull flows. Calculated as density of water multiplied by the gravitational acceleration constant (g), hydraulic radius, and slope ($d \cdot g \cdot R \cdot S$).					
<i>Shear velocity</i> - shear stress at the river bed surface. Calculated as gravitational acceleration (a) multiplied by hydraulic radius and slope ($a \cdot R \cdot S$) ^{0.5} .					
<i>Unit stream power</i> - stream power exerted by the bankfull flow divided by channel width. Calculated as the density of water multiplied by discharge (Q) and slope, and divided by bankfull width ($d \cdot Q \cdot S / Wbkfl$) ^{0.5} ; Where Q = Velocity * A, Velocity = $1.487 \cdot (R^{2/3}) \cdot (S^{1/2}) / n$, and n = Manning's roughness coefficient calculated using equations in Griffiths (1981).					

Table 2.1 (*continued*). Variable definitions and Pearson's correlation coefficients of predictor variables and *P. ceratophyllum* occurrence, length, and their respective principal components. Only coefficients with occurrence and length that are > 0.40 are shown.

	<i>P. ceratophyllum</i> occurrence	Occurrence PC1	<i>P. ceratophyllum</i> length	Length PC1	Length PC2
Sediment Transport (<i>continued</i>)					
<i>Froude number</i> - ratio of inertial to gravitational forces and a measure of water surface roughness. Calculated as $(V^2/(a \cdot \text{depth}))$					
<i>Threshold sediment size</i> - the sediment size at the threshold of movement given the bankfull shear stress. Calculated using Shields' curve, a plot of critical shear stress against sediment size.					
<i>Bed mobility</i> - proportion of the bed in motion at bankfull. Assumes that all sediments smaller than the threshold sediment size are mobilized.	-0.44	0.73			
Sediment Size					
<i>D16</i> - the diameter at which 16% of the sediments are smaller.					
<i>D35</i> - the diameter at which 35% of the sediments are smaller.	0.46				
<i>D50</i> - the diameter at which 50% of the sediments are smaller.	0.53				
<i>D65</i> - the diameter at which 65% of the sediments are smaller.	0.62		0.48		
<i>D84</i> - the diameter at which 84% of the sediments are smaller.	0.62	-0.92	0.66	-0.28	0.89
<i>D95</i> - the diameter at which 95% of the sediments are smaller.	0.54		0.62		
<i>Geometric mean</i> - a measure of central tendency of the data, especially useful for numbers presented as percentages. Calculated as the square root of $D16 \cdot D84$.					
<i>Proportion gravel</i> - proportion of all measured sediments between 2-63 mm.	-0.42		-0.56		
<i>Proportion cobble</i> - proportion of all measured sediments between 64-255 mm.	0.49				
<i>Proportion bedrock</i> - proportion bedrock among all measured sediments.	0.61		0.49		
<i>Proportion fines</i> - proportion of all measured sediments < 2 mm.	-0.41				

Table 2.2. Sample sizes necessary to detect statistically significant differences between entrenched and slightly entrenched sites in the Etowah River. Results are from a power analysis using $\alpha = 0.10$ and power = 0.8.

	Estimated n
Proportion gravel	100
Proportion cobble	114
Proportion fines	624
Occurrence	308
Length	82

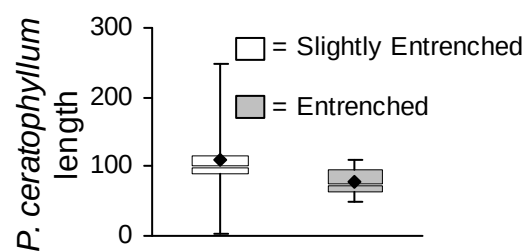
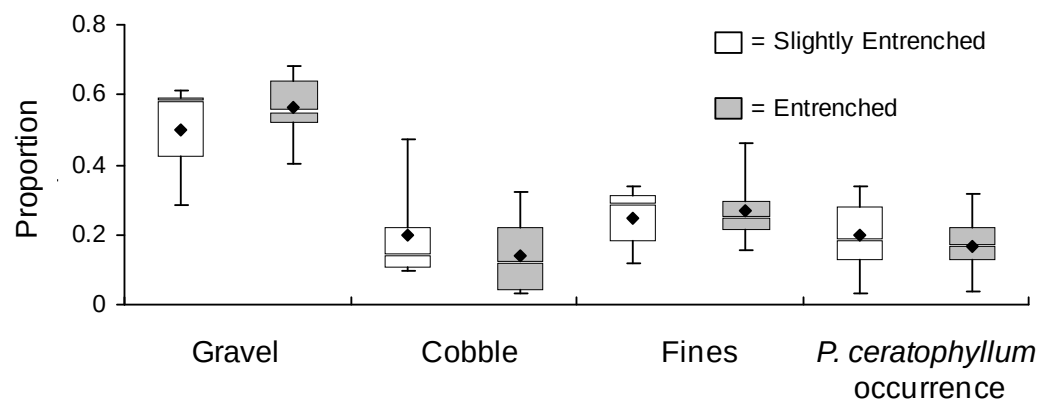


Figure 2.1. Boxplots of habitat variables comparing slightly entrenched channels (open bars) to entrenched channels (gray bars). The top and bottom points in each plot are the maximum and minimum values respectively. The tops and bottoms of the boxes are the lower and upper quartiles for each habitat variable. The diamond within each box represents the median.

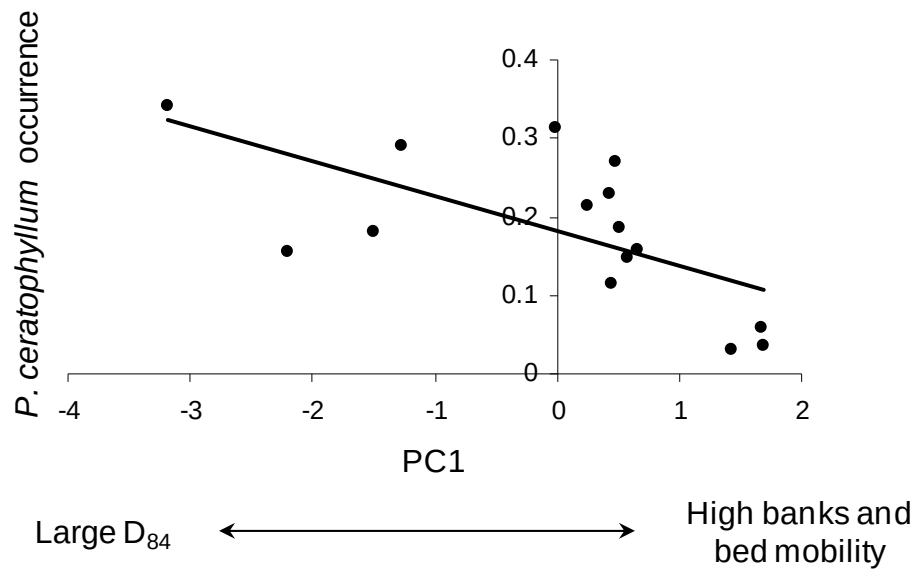


Figure 2.2. Regression of *P. ceratophyllum* occurrence and Principal Component 1 in Etowah River shoals. PC1 accounts for 75.2% of the variation in *P. ceratophyllum* occurrence among sites.

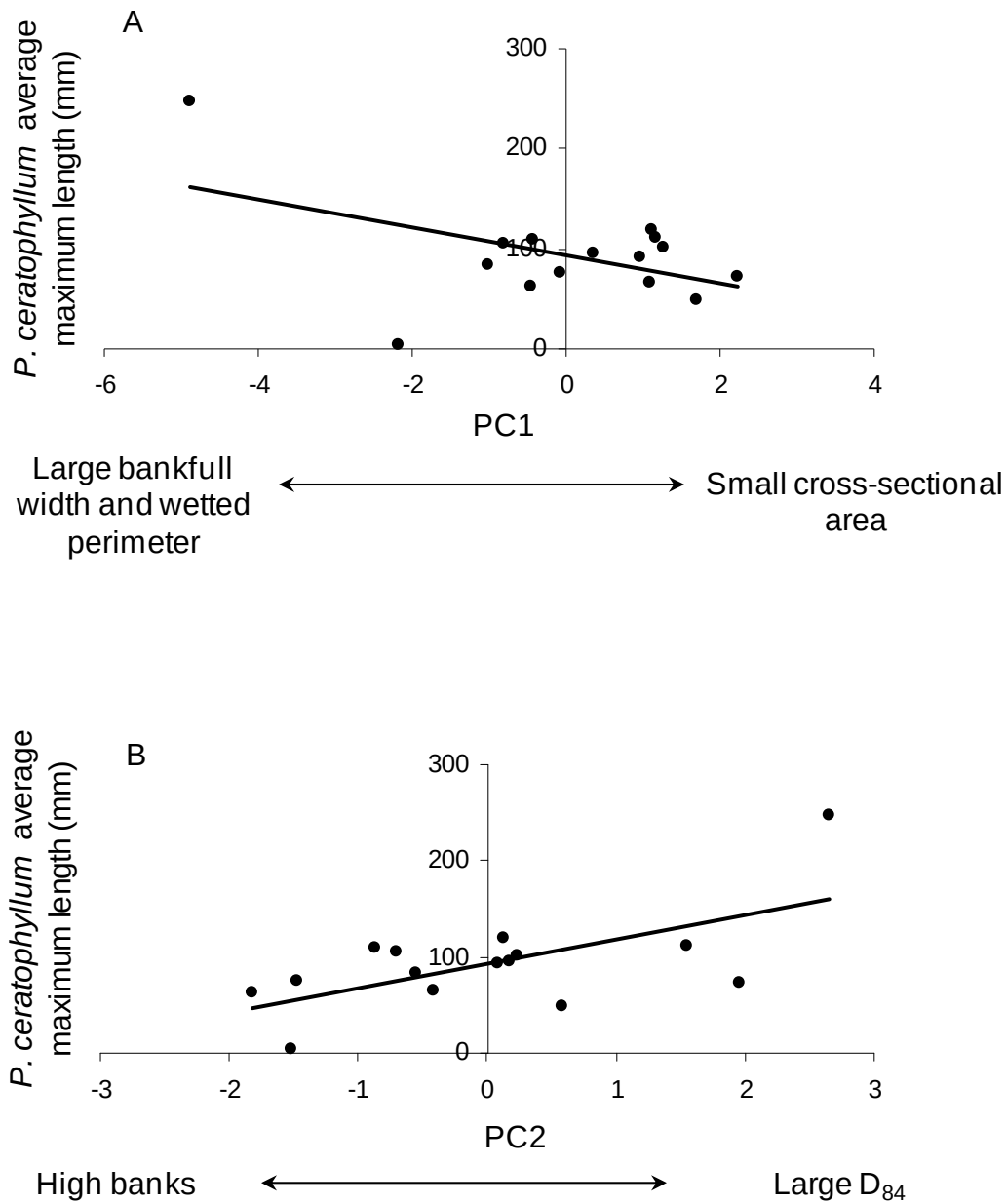


Figure 2.3. Regressions of *P. ceratophyllum* average maximum length and A) Principal Component 1 and B) Principal Component 2 in Etowah River shoals. Length PC1 and PC2 cumulatively account for 64% of the variation in *P. ceratophyllum* length among sites.

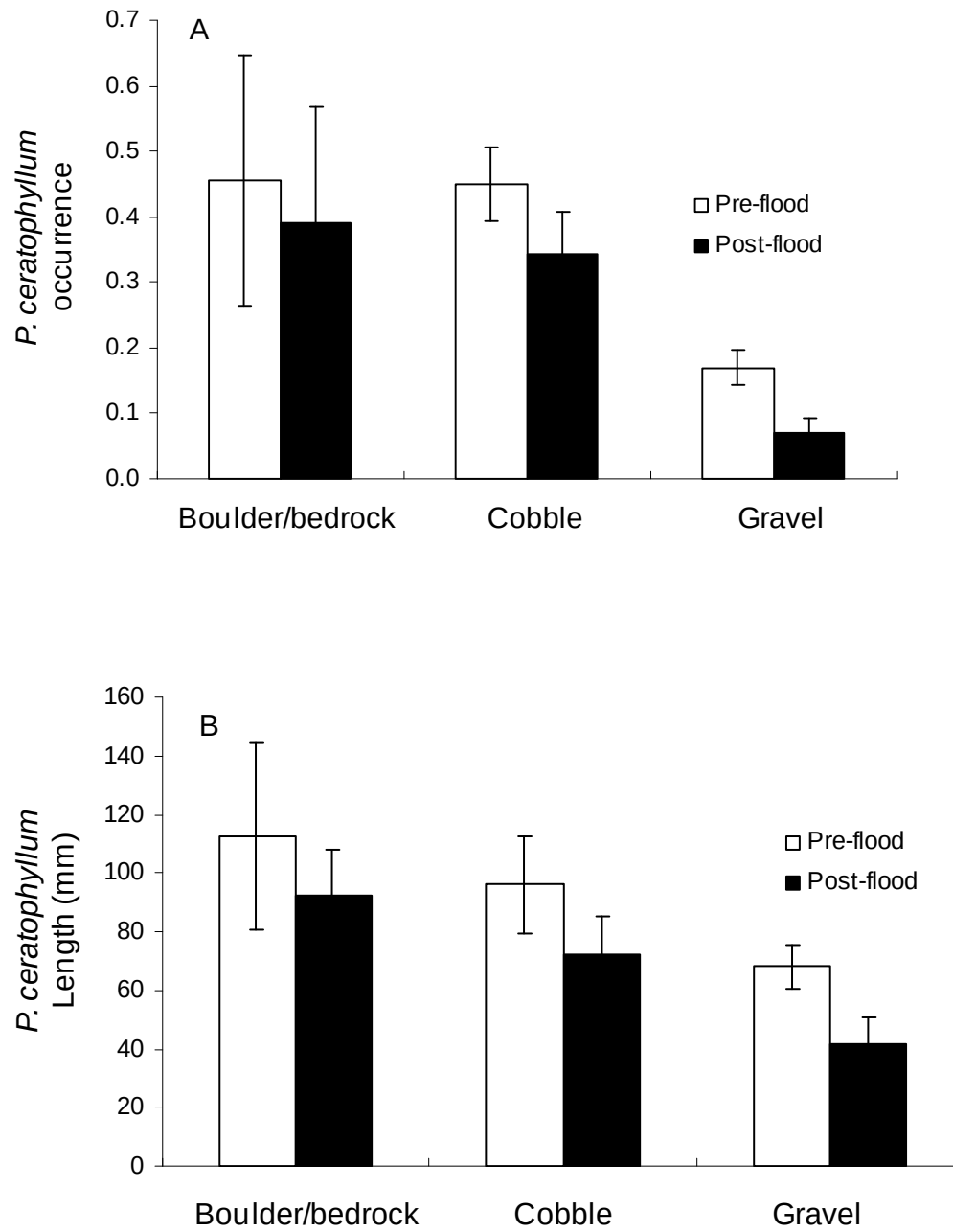


Figure 2.4. *P. ceratophyllum* A) occurrence and B) length in the Etowah River before and after a flood associated with Hurricane Ivan.

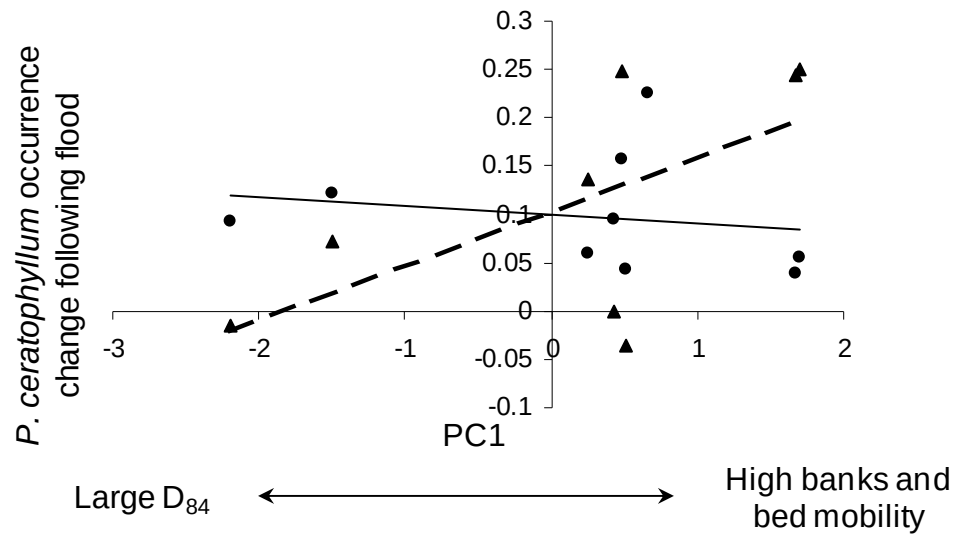


Figure 2.5. Differences in *P. ceratophyllum* occurrence on gravel (solid line, dark circles) and on cobble (dashed line, circles) before and after a flood associated with Hurricane Ivan in the Etowah River plotted against occurrence principal component 1. Lines with different slopes indicate that effects may depend on sediment category. Only the regression of PC1 with cobble is significant ($p = 0.09$).

CHAPTER 3

GEOMORPHIC FACTORS INFLUENCE THE DISTRIBUTION OF A DOMINANT
AQUATIC MACROPHYTE AND AN ENDEMIC CADDISFLY IN A SOUTHEASTERN
RIVER²

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ABSTRACT

Podostemum ceratophyllum (riverweed) is the dominant aquatic macrophyte in riffles and shoals (naturally occurring shallow reaches along a rivercourse) of southeastern streams and rivers. Its ecological role in these systems includes facilitating high macroinvertebrate biomass and creating important habitats for imperiled fishes. Although it is a widespread and ecologically important species, the high level of variation in its morphology and distribution has not been investigated. We hypothesized that channel geomorphology contributed to variation in *P. ceratophyllum* morphology and distribution in the Etowah River, Georgia. We found that *P. ceratophyllum* occurrence increased with channel width and the proportion of bedrock in shoals; these two factors accounted for 77% of the variance in *P. ceratophyllum* occurrence among sites. *P. ceratophyllum* length, a correlate of biomass, increased with basin area and as the proportion of cobble decreased; these two factors accounted for 51% of the *P. ceratophyllum* length variance among sites. Increased channel width correlated with decreased shade but not streambed shear stress. Taken together, shade, water velocity, and sediment size cumulatively accounted for 47%, 32%, and 22% of the variance in *P. ceratophyllum* density, length, and biomass within sites, respectively. Water depth had no effect on density, length, or biomass. *P. ceratophyllum* length was positively correlated with both density and biomass, and density accounted for a majority of the variance (23%) in endemic caddisfly (*Brachycentrus etowahensis*) abundance. Sediment size, water depth and velocity, and shade had no direct effect on caddisfly abundance. This study demonstrates that changes in channel morphology over relatively small distances can have a considerable influence on the distribution of primary producers and associated biota.

INTRODUCTION

Aquatic macrophytes have numerous, important roles in lotic systems. They are important structural components of streams, providing refuge from current for a variety of animals (Giller and Malmqvist 1998), affording stable substrates on which invertebrates colonize (Hynes 1970, Willats 1998), trapping organic matter for consumption by insects (Nelson and Scott 1962, Gregg and Rose 1982), and forming new habitat by facilitating fine sediment deposition (Gregg and Rose 1982) and sediment stabilization (Fritz and Feminella 2003).

Aquatic plant species distributions are highly variable, but reflect, at least in part, instream environmental conditions. Light availability, for example, is important for aquatic plant growth, contributing to the high primary productivity of 3rd-5th order channels and the low primary productivity of forested headwater streams (Vannote et al. 1980). Riparian vegetation has a strong influence on a stream's light regime (Bott 1983), and heavily shaded rivers generally lack plants (Giller and Malmqvist 1998). Additionally, the degree of shade has a strong influence on periphyton biomass, net community primary productivity, nitrogen uptake, and invertebrate abundance (Triska et al. 1983). Thus, light availability plays a fundamental role in the occurrence of some plant species and in ecosystem structure and function.

Channel form may also play an important role in plant distributions, although the effect of channel form on aquatic plants has received less attention than the effect of light availability. Shallow water depths associated with shoals in rivers (i.e., shallow parts of river channels, generally with higher gradient than surrounding channel units) allow more light penetration to bed sediments than surrounding channel units, facilitating primary production. Shoals are generally dominated by large sediments, not only contributing to the diversity and abundance of invertebrates and fish, but also to the proliferation of *Podostemum ceratophyllum* (an aquatic

macrophyte) in Piedmont and Lower Blue Ridge streams in the southeastern U.S. (Nelson and Scott 1962). Moreover, increases in channel width probably result in decreased stream canopy cover and the consequent proliferation of *P. ceratophyllum* (Argentina 2006).

Shoals with similar bankfull discharge but different channel widths can have different shear stress, with narrow shoals having higher shear stress. High shear stress can strongly affect benthic communities. Shear stress controls algal biomass (Townsend and Padovan 2005), the persistence of microorganisms (Silvester and Sleight 1985), insect drift during high flows (Gibbins et al. 2007), and mussel distribution, diversity, and abundance (Howard and Cuffey 2003; Gangloff and Feminella 2007). Shear stress may also affect benthic aquatic macrophytes. Thus, geomorphic variables affecting shear stress may have a strong influence on primary producers and associated biota, mediated by differences in depth, sediment, and width.

We have observed considerable variation in *P. ceratophyllum* occurrence and morphology and *Brachycentrus etowahensis* (Etowah caddisfly) abundance among shoals in the Etowah River (Georgia, USA). Understanding causes of this variation can ultimately aid in the detection and prediction of patterns of macrophyte and caddisfly distributions. Thus, our objective was to determine if geomorphic variation among sites accounts for the observed macrophyte and caddisfly variation in the Etowah River, Georgia. A suite of geomorphic variables were examined for effects on *P. ceratophyllum* occurrence and length. We hypothesized that wide shoals with coarse sediment would contain more macrophytes than narrow shoals with fine sediments. We also expected that *P. ceratophyllum* occurrence and length would increase as basin area decreased, owing largely to the dominance of bedrock in upstream reaches (Appendix B). We tested both shear stress and light availability as mechanisms by which channel width

influences macrophytes, and examined effects of geomorphology, light availability, and *P. ceratophyllum* on endemic, filter-feeding *B. etowahensis* larvae.

METHODS

Study organisms

Podostemum ceratophyllum (riverweed) Michx. is the dominant lotic macrophyte in some rivers of the southeastern United States (Hill and Webster 1984). *P. ceratophyllum* grows predominantly on rocks in shoals. Shoals are shallow parts of river channels (USDA 2003), generally with higher gradients than surrounding channel units. In the Etowah and Conasauga rivers, several imperiled fishes occur in shoals and are more likely to occur in the presence of *P. ceratophyllum* (Freeman et al. 2003, Argentina 2006, Hagler 2006). It increases surface area 3-4 times over bare rock (Hutchens et al. 2004), facilitating high total macroinvertebrate biomass and abundance (Hutchens et al. 2004, Grubaugh and Wallace 1995, Grubaugh et al. 1997).

Brachycentrus etowahensis, the Etowah caddisfly, is endemic to the Etowah River in the Coosa drainage and a small portion of the Tennessee drainage. *P. ceratophyllum* is a critical structural habitat component for *B. etowahensis* larvae, providing a substrate on which it attaches and filter feeds (Willats 1998).

Comparison of *P. ceratophyllum* occurrence and morphology among shoals

Site selection. To assess how shoal geomorphic variation influenced *P. ceratophyllum* occurrence and morphology, we sampled along geomorphic gradients of sediment size and channel width, due to the expected importance of substrate stability (Chapter 2, Argentina 2006) and light availability to *P. ceratophyllum* occurrence and length. We initially surveyed the

locations of all shoals in our study area, visually assessed geomorphic characteristics, and used the visual assessment to stratify more intensive surveys.

We recorded locations of all shoals within a 72 km stretch of the Etowah River (upstream 34° 32' 05.79" N, 84° 03' 47.41" W; downstream 34° 18' 05.54" N, 84° 16' 23.22" W) with a GPS unit during July - September 2005. The downstream boundary of each shoal was determined at base flow as the location at which water depth exceeded 0.6 m, which is the point at which thalweg depth significantly increased in our preliminary shoal investigations. Thus, the upstream extent of shoals was also selected at a water depth of 0.6 m. At each of 216 documented shoals, channel width at mid-shoal was measured using a laser rangefinder (Bushnell Yardage Pro; +/- 1 m accuracy).

Because a quantitative measure of sediment composition was impractical at all shoals, a visual survey of % bedrock, gravel-cobble (combined), and sand was made at 206 of the 216 shoals in 2005. The accuracy of sediment data from the visual survey was tested with quantitative data using Wolman pebble counts (Wolman 1954) at a random selection of 37 shoals during baseflow. Percent bedrock, gravel and cobble, and sand were extracted from the pebble count data, and regression analyses were used to determine how well the visual survey predicted pebble count data. The visual survey predicted actual percent bedrock ($R^2=0.82$), gravel-cobble ($R^2=0.60$), and sand ($R^2=0.18$; $F_{1,36}=155.5$ $p<0.0001$, $F_{1,36}=53.1$ $p<0.0001$, $F_{1,36}=8.0$ $p<0.008$, respectively). Because the visual surveys did not accurately represent actual percent sand, only percent bedrock and gravel-cobble data from the visual survey were used to select sites for more intensive surveys.

Sites were selected for more intensive surveys in 2006 by sampling along the sediment composition and channel width gradients measured in 2005. Because of the large number of

shoals without bedrock (n=119), we selected shoals without bedrock along gradients of width and proportion gravel-cobble. Bedrock shoals were selected along gradients of width and proportion bedrock. To ensure that our selected sampling sites would cover the range of variation in sediment characteristics and widths, all sites were plotted along the sediment and width gradients. The width and sediment axes were divided into fifths and thirds, respectively, to form a grid. Sites within each of the grid cells were then selected for sampling. Because changes in channel gradient from upper river (higher gradient) to lower river (lower gradient) had the potential to influence the distribution of alluvial and bedrock shoals and confound site selection and analysis, we attempted to select sites in both the upper and lower river segments from each grid cell. Although not every grid cell contained a shoal in both river segments, this site selection method ultimately captured a diversity of shoals throughout the river and resulted in a manageable sample size (n=30) for more detailed sampling.

Channel cross-sections. A modified cross-section method (Appendix C) was developed that allowed a single researcher to measure channel dimensions at 25%, 50%, and 75% of the shoal length. The modified method was necessary, as field assistants were largely unavailable to assist in the use of equipment (i.e., stadia, level, and tagline) that requires multiple observers. Dense riparian vegetation and steep channel banks (often 4.5-6 m high) made the use of a tagline and rod to measure cross-sections by a single observer impractical.

We validated the modified cross-section method against a presumably more accurate method- a tagline stretched between banks and tagline height measured using a stadia at nine locations. We used the Hydrologic Engineering Center's River Analysis System (HEC-RAS version 3.1; USACE 2004) to compare cross-sectional area and sediment transport (tons per day) for the two methods at a discharge that reached the top of the lowest bank in the tagline method.

Cross-sectional area and sediment transport were strongly correlated between the two methods (area $R=0.93$ $p=0.0003$; sediment transport $R=0.95$ $p<0.0001$), validating the accuracy of the modified method.

Calculation of hydrologic and geomorphic variables. Channel cross-sections were imported into HEC-RAS (USACE 2004), a program that facilitates calculation of geomorphic parameters at a specified discharge. Because discharge varies among sites depending on drainage area, we standardized our geomorphic calculations by modeling the 2-year recurrence interval discharge (Q_2) given the basin area for each site. Basin area was calculated in ArcView GIS 3.3 software. Q_2 was calculated using empirically derived relationships from rural basins of the upper Piedmont, lower Blue Ridge, and Ridge and Valley physiographic provinces of north Georgia (USGS 1999). Q_2 estimates were calibrated using stream flow data from an existing downstream gage (USGS gage 02392000) and by using weighted estimates from Stamey and Hess (1993; USGS 1999).

HEC-RAS was used to calculate channel width, shear stress, wetted perimeter, hydraulic radius, maximum channel depth, and flow area for each channel cross section for the Q_2 estimate. Values were averaged for each of the three cross-sections to represent each site.

Sediment, *P. ceratophyllum* occurrence, and length measurements. Wolman pebble counts were used to measure size of a minimum of 100 sediment particles per shoal (Wolman 1954). Counts were conducted along 10-12 transects equidistantly spaced to span the entire shoal length. To characterize instream habitat, bank sediments were not included in the pebble count. Habitat variables derived from the pebble counts included the proportion of fines (≤ 2 mm), gravel (2-63 mm), cobble (64-255 mm), D_{50} and D_{84} (the diameters at which 50% and 84% of the particles are smaller, respectively) for each site.

Each particle collected in the pebble count was visually assessed for the presence of *P. ceratophyllum*. Because of the large number of plant stems on any one particle and the impracticality of measuring multiple stems or biomass, maximum plant length was recorded. Maximum length provided a standardized, repeatable measure of plant morphology. Thus, *P. ceratophyllum* variables for each site included average maximum length and frequency of occurrence (calculated as the proportion of all particles with *P. ceratophyllum* present).

Analysis. A correlation matrix was used to assess relationships among geomorphic predictor variables and *P. ceratophyllum* occurrence and length among shoals. Suites of predictor variables that showed a high level of relatedness were represented by the variable that showed the strongest correlations with *P. ceratophyllum* occurrence and length. These variables were included in forward stepwise multiple linear regression analysis to calculate partial and cumulative R^2 values in SAS version 8 (SAS Institute, Cary, NC).

Factors affecting *P. ceratophyllum* biomass, length, and *B. etowahensis* abundance within shoals

A subset of sampled shoals was chosen for more detailed investigation of the effects of depth, velocity, shade, and sediment size on *P. ceratophyllum* density, biomass, and length, and caddisfly abundance (July - August 2006). Five shoals from the previous survey were selected in Dawson Forest based on accessibility. Three transects across each shoal were established, corresponding to the channel cross-sections. Preliminary studies indicated that sampling intervals of 3 m were adequate to minimize autocorrelation of the shade variable among sampling locations, starting at a random location between 1 and 3 m from the bank. This sampling design resulted in a total of 128 sampling locations among the five shoals.

A clinometer was used to measure the total number of degrees where the channel would be shaded by vegetation throughout the day as the sun tracked from sunrise to sunset in the growing season (July-August). Thus, these measurements were taken largely in an east-west direction while taking into account the sun angle and azimuth. A totally shaded location would have a value of 180°. Water depth and velocity were recorded at each location using a Marsh-McBirney velocity meter and wading rod.

At each location along the transect, a 222.8 cm² *P. ceratophyllum* sampler, similar in design to a Surber sampler, was placed on the streambed. The sampler was divided into nine equally sized sections and the presence/absence of *P. ceratophyllum* in each section was recorded as a measurement of *P. ceratophyllum* density. The intermediate axis of the largest sediment particle within the sampler was recorded, as it was the most likely to influence *P. ceratophyllum* density and had the potential to be located in more than one section. *P. ceratophyllum* was removed by hand from sediments and allowed to drift into the sampler until all that remained were the firmly attached roots. In the lab, samples were rinsed to remove sediment, maximum *P. ceratophyllum* length was measured, and Etowah caddisflies were counted. *P. ceratophyllum* samples were dried at 50°C until constant dry mass was recorded. Samples were weighed before and after ashing at 550°C to determine ash free dry mass (AFDM), a biomass estimate.

Analysis. *P. ceratophyllum* predictor variables (sediment size, shade, depth, velocity) measured at the 5 shoals were not correlated. Thus, all were included in a single model to assess whether they had a significant affect on *P. ceratophyllum* density, length, and AFDM using PROC GLM in SAS. Site was introduced as a class variable to account for site-level effects. If site and other variables had no effect on *P. ceratophyllum* density or caddisfly abundance, they were removed

from the analysis and forward stepwise multiple linear regression analysis was used to calculate partial and cumulative R^2 values.

A similar analysis was used to test for effects on caddisfly abundance, but included additional predictor variables (*P. ceratophyllum* length, AFDM, and density). Predictor variables were screened for correlation and if correlated, the variable with the largest correlation coefficient with caddisfly abundance was chosen for the analysis.

Average shade from all samples at a site was calculated. Linear regression analysis was used to test average channel width as a predictor of a site's average degree of shade and average shear stress.

RESULTS

P. ceratophyllum occurrence and length among shoals

Neither shear stress nor basin area was correlated with *P. ceratophyllum* occurrence (Table 3.1). However, *P. ceratophyllum* occurrence increased as the proportion of bedrock and channel width increased. Correlation analysis indicated multiple predictor variables were correlated with *P. ceratophyllum* occurrence (Table 3.1); but the proportion of sediments that were bedrock ($R = 0.85$, $p < 0.0001$) and mean channel width ($R = 0.40$, $p = 0.04$) had the highest correlation coefficients with *P. ceratophyllum* occurrence (Table 3.1). Although basin area was correlated with the proportion of bedrock and mean channel width, bedrock and width were not correlated ($R = 0.17$, $p = 0.39$) and were retained in multiple linear regression analysis. The proportion of bedrock and shoal width explained 77% of the total variance in *P. ceratophyllum* occurrence among sites (Figure 3.1; bedrock $R^2 = 0.70$, $F_{2,25} = 56.8$, $p < 0.0001$; width $R^2 = 0.07$, $F_{2,25} = 6.92$, $p < 0.02$).

P. ceratophyllum length increased as the proportion of cobble decreased and basin area increased. Correlation analysis indicated multiple variables were correlated with *P. ceratophyllum* length (Table 3.1), but the proportion of cobble, basin area, and channel depth had the highest correlation coefficients with *P. ceratophyllum* length ($R = -0.45$ $p < 0.01$; $R = 0.63$ $p < 0.0002$; $R = 0.64$, $p = 0.0004$, respectively). Basin area and maximum channel depth at bankfull were correlated ($R = 0.97$ $p < 0.0001$). Because shoal basin area can be calculated without field measurements, it is more useful than maximum channel depth at bankfull to estimate *P. ceratophyllum* length at unmeasured sites. Therefore, it was chosen for the multiple linear regression analysis. Basin area and proportion cobble explained 51% of the variance in *P. ceratophyllum* length (Figure 3.2; basin area $R^2 = 0.48$, $F_{2,28} = 17.9$, $p < 0.0001$; proportion cobble $R^2 = 0.12$, $F_{2,28} = 6.17$, $p = 0.02$).

P. ceratophyllum biomass, length, and *B. etowahensis* abundance within shoals

Within shoals, neither site nor depth affected any of the response variables measured and were, therefore, removed from the analysis. Multiple regression analysis indicated that velocity, sediment size, and shade, taken together, accounted for 47% of the variance in *P. ceratophyllum* density, 32% in length, and 22% in AFDM (Table 3.2) within a site.

P. ceratophyllum density was positively correlated with both AFDM ($R = 0.57$, $p = 0.0001$) and length ($R = 0.80$, $p = 0.0001$), and length was correlated with AFDM ($R = 0.69$, $p < 0.0001$; Appendix D). Of these three variables, *P. ceratophyllum* density had the highest correlation coefficient with caddisfly abundance ($R = 0.48$, $p < 0.0001$). Therefore, *P. ceratophyllum* density was retained among the other predictors (sediment size, shade, depth, and

velocity) to examine effects on caddisfly abundance. However, only *P. ceratophyllum* density accounted for a significant portion (23%) of the variance in caddisfly abundance (Table 3.2).

Average cross section width at the five sites predicted average degrees of shade for a site (Figure 3.3: $R^2=0.71$, $F_{1,4}=7.5$ $p=0.07$), but not shear stress ($R^2=0.20$, $F_{1,4}=0.8$ $p=0.44$).

DISCUSSION

Podostemum ceratophyllum occurrence among shoals increased as the proportion of bedrock in shoals and channel width increased, although bedrock had the strongest influence. Occurrence decreases with proportion gravel and fines are likely a statistical artifact; proportion gravel and fines increase as bedrock decreases. These results support previous studies in this system showing that *P. ceratophyllum* occurrence increases with sediment size (Chapter 2). Mobilization of smaller particles during high flow events, and the subsequent removal of *P. ceratophyllum* stems during particle mobilization, could result in lower *P. ceratophyllum* occurrence on smaller particles.

Channel width was a significant predictor of *P. ceratophyllum* occurrence among shoals. This supports our hypothesis that wider shoals have more macrophytes. However, unlike other studies that showed shear stress effects on primary producers (Townsend and Padovan 2005), we found no relationship between shear stress and *P. ceratophyllum* occurrence among shoals at high flow (Table 3.1), indicating that factors other than sediment transport make channel width a relevant predictor of this species' distribution.

We evaluated shade and shear stress as potential mechanisms through which channel width influences *P. ceratophyllum* density and biomass, and Etowah caddisfly abundance. Shear stress was not correlated with average channel width. Therefore, it is unlikely that the effects of

channel width on *P. ceratophyllum* density or biomass are mediated by shear stress. However, shade increased as channel width decreased (Figure 3.2) resulting in reduced average *P. ceratophyllum* density. *P. ceratophyllum* density was the best predictor of *B. etowahensis* abundance within shoals. Because *B. etowahensis* is a filter feeder, increases in abundance are not mediated by a trophic relationship between *P. ceratophyllum* and the caddisfly. Rather, abundance increases are likely attributed to the macrophyte as a structural ecosystem component (e.g. Hynes 1970, Willats 1998). These relationships implicate channel width as a dominant geomorphic factor that controls shade, primary producers, and the abundance of taxa that depend on the habitat provided by primary producers.

P. ceratophyllum length declined as the proportion of cobble sediment increased and as basin area decreased. The inverse relationship between proportion cobble and bedrock, and the strong positive correlation of *P. ceratophyllum* length with bedrock, D_{50} , and D_{84} are indications that *P. ceratophyllum* length increases as sediment size increases. Similar to the *P. ceratophyllum* density results, large sediments are more stable during high flows. Therefore, they also may be more conducive to plant growth.

We expected that average of *P. ceratophyllum* maximum lengths at a site would increase as basin area decreased, owing largely to the high proportion of bedrock sediments in upstream shoals. However, we observed a strong relationship in the opposite direction; *P. ceratophyllum* stems were longer at downstream (greater basin area) shoals. The increase in *P. ceratophyllum* length with basin area could be a consequence of changes in the physicochemical characteristics of the water. Water temperature generally increases in a downstream direction (Hynes 1970), and water temperature changes alter plant physiology, distribution, and nutrient uptake (Lambers et al. 1998). Nutrient levels may also increase downstream as a consequence of increased runoff,

and may have substantial effects on aquatic plant growth (Cushing and Allan 2001, Hillebrand 2002). Although differences in water physicochemical factors are plausible mechanisms explaining morphological differences between plants at upstream and downstream sites, we cannot rule out genetic differences between plant populations in upstream and downstream locations. Because variation in water temperature or nutrient loads was not measured at these sites, we cannot determine if this variation explains the variation measured in *P. ceratophyllum* length.

P. ceratophyllum biomass and maximum length were positively correlated. Because measurements of *P. ceratophyllum* length are more efficient than measurements of biomass, using length as a surrogate for biomass may be a useful technique for comparing biomass among samples and among shoals.

Combined, these results suggest that basin area and variations in channel morphology strongly influence *P. ceratophyllum* distribution and morphology, and ultimately influence invertebrate communities through non-trophic mechanisms. Factors that control channel width and sediment size variation should be studied to improve our understanding of macrophyte distributions in riverine systems.

IMPLICATIONS FOR PRACTICE

- Differences in channel width, shade, sediment composition, and basin area should be considered when comparing *P. ceratophyllum* among shoals.

- Because measurements of *P. ceratophyllum* length are more efficient than measurements of biomass, using length as a surrogate for biomass may be a useful technique for comparing biomass among samples and among shoals.

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Table 3.1. Correlation coefficients of *P. ceratophyllum* occurrence and length with potential predictor variables. All coefficients are significant at $p < 0.05$ or are not significant (NS). Variables that are grouped in bold boxes are correlated with one another.

	Fines	Gravel	Cobble	Bedrock	D ₅₀	D ₈₄	Basin Area	Q ₂
Occurrence	-0.57	-0.72	NS	0.85	0.64	0.68	NS	NS
Length	0.34	NS	-0.45	NS	NS	NS	0.63	0.55

	Mean Width	Surface Width	Wetted Perimeter	Shear Stress	Hydraulic Radius	Channel Depth
Occurrence	0.41	0.41	0.36	NS	NS	NS
Length	0.51	0.51	0.54	0.46	0.61	0.64

Table 3.2. Multiple regression statistics for response variables *P. ceratophyllum* density, length, ash free dry mass (AFDM), and Etowah caddisfly (*Brachycentrus etowahensis*) abundance. Partial R^2 values are presented for each predictor variable (velocity, sediment size, and degrees of shade) and sum to the cumulative R^2 value, or are not significant (NS) at $p < 0.05$.

		Velocity	Sediment Size	Shade	Cumulative R^2	<i>P. ceratophyllum</i> density
<i>P. ceratophyllum</i> density	R^2	0.10	0.08	0.29	0.47	
	$F_{3,123}$	20.6	18.5	49.0		
<i>P. ceratophyllum</i> length	R^2	0.04	0.20	0.08	0.32	
	$F_{3,123}$	7.8	29.8	12.8		
<i>P. ceratophyllum</i> AFDM	R^2	0.04	0.06	0.12	0.22	
	$F_{3,123}$	6.0	8.2	17.2		
Etowah caddisfly abundance	R^2	NS	NS	NS		0.23
	$F_{1,123}$	NS	NS	NS		37.1

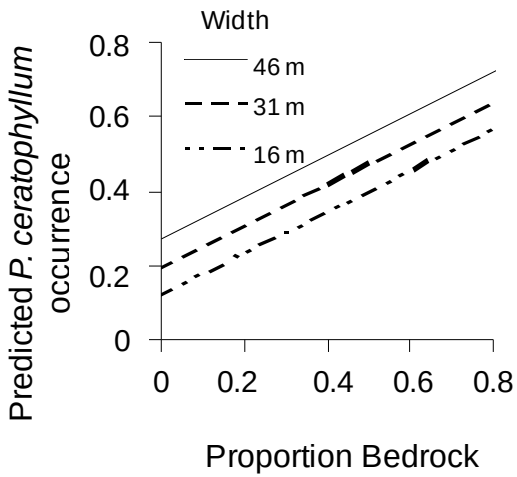


Figure 3.1. Relationships between modeled proportion of bedrock and predicted *P. ceratophyllum* occurrence at the minimum (16 m), median (31 m), and maximum (46 m) channel widths measured, and The positive relationship between proportion bedrock (b), mean channel width (w , meters), and *P. ceratophyllum* occurrence (y_o) can be explained by the following equation: $y_o = 0.56*b + 0.005*w + 0.04$.

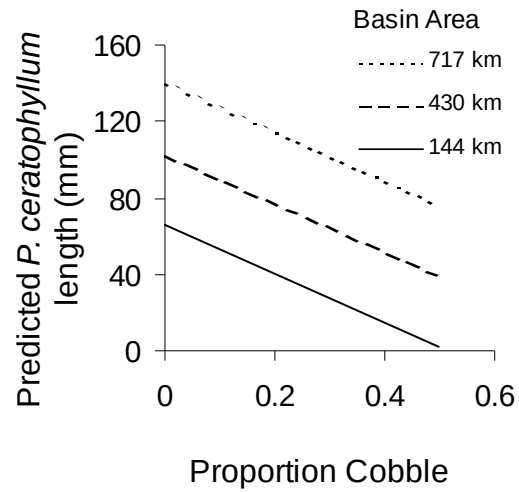


Figure 3.2. Relationships between modeled proportion of cobble and predicted *P. ceratophyllum* length at minimum (144 km²), median (430 km²), and maximum (717 km²) basin areas measured. The relationship between basin area (a , km²), proportion cobble (c), and *P. ceratophyllum* length (y_o , mm) can be explained by the following equation: $y_L = 0.13*a - 127.0*c + 46.9$.

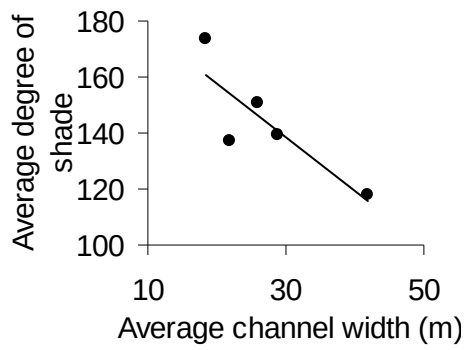


Figure 3.3. Relationship between average channel width and average degree of shade in the Etowah River ($R^2 = 0.71$, $F_{1,4} = 7.5$, $p = 0.07$). Each point represents the average of 3 transects within a shoal. The relationship between average channel width (w) and average shade (s) can be explained by the following equation: $s = -0.59(w) + 196.7$.

CHAPTER 4

LARGE CHANNEL CONFLUENCES INFLUENCE GEOMORPHIC HETEROGENEITY OF
A SOUTHEASTERN RIVER³

³W.W. Duncan, G.C. Poole, and J.L. Meyer. To be submitted to *Water Resources Research*.

ABSTRACT.

Detection of biological patterns in structurally complex rivers is difficult but essential in the management of imperiled species. Based on the Network Dynamics Hypothesis (NDH), we predicted that tributaries exert a strong influence on mainstem morphology, mediated by tributary sediment inputs. We predicted that the likelihood that a tributary will affect mainstem geomorphology depends on the ratio of the tributary basin area to the mainstem basin area ($T_{BA}:M_{BA}$). Although the results of this study do not indicate that $T_{BA}:M_{BA}$ is a useful predictor of shallow alluvium-dominated confluences (i.e., shoals) in the Etowah River, alluvial shoals were closer to tributary mouths than were other shoal types, indicating an association with tributaries. Shoals near large tributary confluences also contained a larger proportion of gravel and cobble bed sediments and were wider than adjacent, downstream shoals. These confluence-associated shoals may be ecologically different, in that aquatic macrophyte occurrence is higher in wide shoals with coarse sediments. Recognizing confluence-associated shoals as unique shoal types may aid researchers in understanding the distribution patterns of aquatic organisms.

INTRODUCTION

River channel geomorphology and position within the river network influence species distributions (Allan 2004, Vannote et al. 1980, Ward and Stanford 1995). In large river systems where species distributions are spatially and temporally variable, distinctive biological patterns are difficult to detect. As a result, sampling is often stratified according to predetermined classification schemes (e.g. riffle, run, pool; Kaufmann et al. 1999) or dominant disturbance type (Montgomery 1999; Pringle et al. 1988). Although these classifications aid in experimental design and sample stratification, they are insufficient in that the classifications cannot be used to

predict habitat locations or account for the considerable geomorphic variability that exists within each class. For example, riffle slope, bed texture, and channel width vary considerably among river segments and reaches. These geomorphic differences undoubtedly influence biological communities because slope, bed texture, and channel width are important habitat variables for aquatic macrophytes (Suren and Duncan 1999), insects (Roy et al. 2003) and fishes (Sutherland 2002, Vogt 2004, Walters et al. 2003).

Tributary junctions contribute to ecological heterogeneity in river systems. Longitudinal gradients in functional composition of macroinvertebrate communities and organic matter transport are modified by tributaries, but the effect depends on tributary size (Bruns et al. 1984). Tributaries increase coarse sediment inputs, resulting in macroinvertebrate communities that are distinct from other riffles (Rice et al. 2001). Electric fish (*Gymnotiformes*) species richness increases in a downstream direction in the Amazon River, but diversity increases are punctuated below tributary confluences (Fernandes et al. 2004). Thus, confluences may have a significant influence on river ecology, yet their role in ecosystem structure and function remains relatively unstudied.

Over large spatial scales, bed texture and slope decrease, and width increases in a downstream direction (Vannote et al. 1980), but considerable geomorphic variation exists in part due to lateral sediment inputs. Bed texture fining is punctuated by particle size increases near confluences (Church and Kellerhals 1978; Knighton 1998; Troutman 1980). Coarse sediment inputs can shift meandering planforms to braided ones (Galay et al. 1998). Tributary sediment inputs can increase channel slope, thereby increasing shear stress below tributaries (Rice et al. 2001). Because flows may increase significantly at confluences, channels may widen, increasing light availability and primary and secondary productivity (Rice et al. 2001).

Not all tributaries have an ecological or geomorphic effect, and unifying characteristics of those tributaries that do are difficult to determine (Rice 1998). Thus, geomorphic “punctuation” is likely to vary spatially and temporally among confluences depending on climatic and geomorphic factors that influence hydrology and sediment transport from tributaries to larger channels. However, the likelihood of a tributary interrupting downstream hydrologic and geomorphic trends is expected to be a function of tributary size relative to the mainstem (Rice et al. 2001, Benda et al. 2004a).

Accordingly, the Network Dynamics Hypothesis (NDH; Benda et al. 2004a, 2004b) relates tributary geomorphology to the occurrence of alluvial fans and shallow, alluvial channel units at confluences. One prediction based on the NDH, is that confluences with large tributary to mainstem basin area ratios ($T_{BA}:M_{BA}$) have a higher potential to transport coarse sediments into transport-limited reaches, resulting in coarse sediment accumulation and altered geomorphology at confluences (i.e., a confluence effect). These shallow, alluvium-dominated landforms near confluences may be geomorphically distinct from other shallow, alluvial landforms because confluences often have higher shear stress and slope (Rice et al. 2001). Although the likelihood of a confluence effect increases with $T_{BA}:M_{BA}$ in montane western North American drainages (Benda et al. 2004a), we are unaware of studies assessing $T_{BA}:M_{BA}$ outside of western North America. $T_{BA}:M_{BA}$ in other regions may be a useful predictor of unique habitat locations and may account for ecological and geomorphic variation among sites. Such an approach is appealing because of the inherent variability of riverine environments and the difficulty in detection of ecological patterns.

Thus, we set out to examine the effects of tributaries on channel geomorphology in a southeastern river. Our research objectives were to 1) identify the relationship between

confluence location and alluvial shoal occurrence using $T_{BA}:M_{BA}$ and T_{BA} , and 2) determine if there is a geomorphic difference between confluence-associated shoals and other shoals.

Study system

We studied the predictions associated with the Network Dynamics Hypothesis and the geomorphic significance of confluence-associated shoals in the Etowah River in north Georgia (USA). Shoals are shallow parts of river channels (USDA 2003), generally with higher gradients than surrounding channel units. Shoals in the Etowah River above Lake Allatoona are biologically diverse, harboring both state and federally listed species such as the Etowah darter (*Etheostoma etowahae*), amber darter (*Percina antesella*), freckled darter (*Percina lenticula*), “Coosa” madtom (*Noturus* sp. cf. *N. munitus*), and endemic Etowah caddisfly (*Brachycentrus etowahensis*). The occurrence of several imperiled fishes increases in the presence of *Podostemum ceratophyllum* (Freeman et al. 2003, Hagler 2006), an aquatic macrophyte that grows on rocks. The high species diversity, large number of imperiled species, and presence of ecologically important shoal habitats make the Etowah River an important location to study geomorphic variation and test predictions associated with the Network Dynamics Hypothesis.

The upper part of the study area (from SR52 to SR136) is of higher gradient and contains more bedrock, whereas the lower river (SR136-Yellow Creek Rd) is of lower gradient and contains more alluvium (Figure 4.1). Geology of tributaries in both the upper and lower river segments is of metamorphic origin, primarily comprising moderate to high grade gneiss and schist (Appendix E, German 1985). Biotite, muscovite, amphibolite, and quartz are minerals common to most tributaries. Numerous other minerals occur and may add geologic diversity among tributaries (Appendix E, German 1985). However, large portions of tributary basins were

not geologically mapped, thus hindering contrasts of tributary geology. Alluvial processes are the dominant domain (*sensu* Montgomery 1999) of the Etowah River study area. Because channel gradient influences sediment transport, major changes in channel slope delineate river segments. Consequently, shoals in the Etowah River are highly diverse in their morphology, ranging in width, sediment composition, average tractive force, and light availability. This morphological diversity is a probable cause of highly variable *P. ceratophyllum* and fish occurrence in the Etowah River (Chapter 2, Freeman et al. 2003). Additionally, preliminary observations of Etowah River shoal locations indicated that many of the shoals dominated by gravel and cobble occurred in close proximity to large, upstream tributary confluences.

METHODS

Locations of all shoals within a 72 km stretch of the Etowah River were recorded with a GPS unit during summer and fall 2005. At each of 216 documented shoals, channel width at mid-shoal was measured using a laser rangefinder (Bushnell Yardage Pro; ± 1 m accuracy).

A visual survey of % bedrock, gravel-cobble (combined), and sand was made at each shoal in 2005. Accuracy of the visual survey was assessed with quantitative data using Wolman pebble counts (Wolman 1954) at a random subset of 38 shoals during baseflow. Percent bedrock, gravel and cobble, and sand were extracted from the pebble count data, and regression analyses were used to determine how well the visual survey data predicted pebble count data. The visual survey predicted percent bedrock, gravel-cobble, and sand at $R^2=0.82$, $R^2=0.63$, and $R^2=0.18$ ($p < 0.05$ for all regressions). Because visual surveys did not accurately estimate the percentage of sand, only % bedrock and gravel-cobble data from the visual survey were used in subsequent analyses.

Hierarchical cluster analysis (JMP, Version 7. SAS Institute Inc. Cary, NC, 1989-2007) was used to group shoals according to similar % bedrock and % gravel-cobble. Shoal clusters with high % gravel-cobble and low % bedrock (which we term ‘alluvial shoals’) were the focus of additional analysis because this shoal type is most likely to be formed by tributary sediment inputs.

Basin areas for all tributaries and confluences within the 72 km river reach were calculated using ArcView GIS 3.3 software, and tributary to mainstem basin area ratios ($T_{BA}:M_{BA}$) were calculated (Benda et al. 2004a, 2004b). Logistic regressions (Proc GENMOD, SAS version 8, SAS Institute, Cary, NC) were used to test whether alluvial shoals were more likely to be present as T_{BA} or $T_{BA}:M_{BA}$ ratios increased. Shoal presence was determined within distance categories of 0-50 m, 0-100 m, 0-150 m, and 0-200 m downstream of a tributary confluence, and separate logistic regression analyses were used on each category. Because tributaries with basin areas $< 1 \text{ km}^2$ are unlikely to affect geomorphology of mainstem rivers $> 50 \text{ km}^2$ (Benda et al. 2004), the analysis was repeated while excluding tributaries with basin areas $< 1 \text{ km}^2$.

To test whether alluvial shoals were closer to tributary confluences than other shoal clusters, we calculated the distances between confluences and the nearest downstream shoal in each sediment cluster. In cases where another confluence was encountered before the nearest downstream shoal (i.e., two or more tributaries above one shoal), an average distance, weighted by tributary basin area was used in the analysis. All other factors being equal, larger tributary basins are apt to convey larger quantities of sediment and have a greater propensity for producing confluence effects (Rice et al. 2001, Benda et al. 2004). Thus, the weighted distance is an adjusted distance that takes into account the influence of both tributaries, while more

heavily weighting the distance to the larger tributary. Weighted distances (D_w) were calculated as

$$D_w = (D_1 * A_1 + D_2 * A_2 + D_3 * A_3) / (A_1 + A_2 + A_3);$$

where D_w is weighted distance (m), D_1 is distance between tributary 1 and the shoal and A_1 is the basin area for tributary 1. To compare distances from confluences to shoals among shoal clusters, we used a two-way ANOVA that included river segment and shoal cluster as main effects. Weighted distance data were log-transformed. Differences among means were explored using Tukey's HSD test. Because there were many more alluvial shoals than other shoal types (Table 4.1), smaller distances from confluences to alluvial shoals could be caused by sample size differences. Thus, if the two-way ANOVA indicated significant differences in distances from confluences to shoals among shoal clusters in a river segment, distances from confluences to alluvial shoals were compared to distances from confluences to uniformly spaced points. The number of uniformly spaced points equaled the number of alluvial shoals in that river segment. Distances to shoals were compared to uniformly spaced points using a Kruskal-Wallis non-parametric test. A significant difference was an indication that shoal locations were non-uniformly distributed throughout the river, and that their proximity to confluences compared to other shoal types was not necessarily driven by sample size.

Because confluences with large $T_{BA}:M_{BA}$ ratios are the most likely to affect mainstem morphology (Benda et al. 2004a), we examined the largest 10% of $T_{BA}:M_{BA}$ ratios ($n = 11$ confluences) in more detail. Of these, six had shoals immediately downstream and five did not. We hypothesized that tributary % gravel-cobble and slope might help explain the difference

between tributaries with and without immediate downstream shoals because both tributary slope and sediment size are major determinants of tributary sediment export (sensu Rice et al. 2006). Therefore, we measured these two variables and determined if they served as good predictors of shoal occurrence and sediment size. Tributary sediment size was assessed using the Wolman pebble count (Wolman 1954) in a reach length that was 20 times stream width. The sampled reach was located upstream from the downstream-most tributary riffle, as the riffle was the first alluvial feature encountered that was formed by the tributary and presumably outside the influence of mainstem fine sediment deposition at high flows. Slope was measured using 7.5 minute USGS topographic maps. Logistic regression was used to assess tributary % gravel-cobble and slope (in one logistic regression model) as predictors of shoal occurrence within 200 m downstream from the confluence. Multiple regression analysis was used to predict confluence % gravel-cobble (from visual survey) from tributary % gravel-cobble and slope.

We tested whether shoals below large tributary confluences (hereafter termed ‘confluence-associated shoals’) contribute to reach scale geomorphic variation in channel width and sediment composition. The largest 10% of all $T_{BA}:M_{BA}$ ratios with shoals less than 200 m below their confluence ($n = 6$) were selected. To avoid confounding factors associated with reach scale differences, including changes in basin topography and flow, comparisons were made of width, % bedrock, and % gravel-cobble between the confluence-associated shoal and its nearest downstream shoal. Similar comparisons were made between confluence-associated shoals and the nearest downstream shoal in the same sediment cluster. Paired t-tests were used to compare sediment composition from the visual survey and width measurements.

RESULTS

Hierarchical cluster analysis on sediment data from visual surveys resulted in four shoal clusters: 1) shoals composed of alluvial sediments with little or no bedrock (i.e., alluvial shoals), 2) moderate alluvium and low bedrock shoals, 3) low alluvium and high bedrock shoals, and 4) moderate alluvium and moderate bedrock shoals. The latter two clusters were combined because of similarity of sediment composition and low number of shoals in those clusters resulting in three distinct shoal clusters: high alluvium, high bedrock, and moderate bedrock/moderate alluvium (Figure 4.2, Table 4.1).

Alluvial shoals were not more likely to occur as T_{BA} or $T_{BA}:M_{BA}$ ratios increased, regardless of distance category below the confluence (the best logistic regression statistic was $T_{BA}:M_{BA}$ and presence 0 - 50 m; $X^2_{(1)} = 0.43$, $p = 0.51$). When tributaries with basin areas $< 1 \text{ km}^2$ were excluded from the analysis, shoals were not more likely to occur as T_{BA} or $T_{BA}:M_{BA}$ ratios increased, regardless of distance category below the confluence (the best logistic regression statistic was $T_{BA}:M_{BA}$ and presence 0 - 50 m; $X^2_{(1)} = 0.61$, $p = 0.43$).

Shoal clusters differed in their weighted distances from confluences to shoals depending on river segment (segment $F_{1,103} = 2.28$, $p = 0.13$; cluster $F_{2,103} = 9.56$, $p = 0.0002$; segment*cluster $F_{2,103} = 8.29$, $p = 0.0005$; Figure 4.3). In the lower river segment, alluvial shoals were closer to confluences than were other shoal clusters (Figure 4.3: $F_{2,54} = 17.7$, $p < 0.0001$), and distances from confluences to alluvial shoals in the lower river were less than distances to an equal number of equidistantly spaced points ($X^2_{(1)} = 7.46$, $p = 0.006$; Figure 4.4). However, there were no significant differences in distances between confluences and shoals among clusters in the upper river segment ($F_{2,48} = 1.91$, $p = 0.16$). Tributary % gravel-cobble and slope did not

predict shoal occurrence ($X^2_{(1)} = 0.08$ $p = 0.77$ and $X^2_{(1)} = 1.29$ $p = 0.26$, respectively), nor did they predict % gravel-cobble at the confluence ($R^2 = -0.18$, $F_{2,10}=0.15$, $p = 0.86$).

Shoals below the six largest tributary confluences had more gravel-cobble, less bedrock, and were wider than the nearest downstream non-confluence shoal (width $t_{(5)} = 1.72$, $p = 0.06$; bedrock $t_{(5)} = 1.99$, $p = 0.04$, gravel-cobble $t_{(5)} = 2.41$, $p = 0.02$; Figure 4.5). When compared to downstream shoals in the same shoal cluster, they were also significantly wider ($t_{(5)} = 5.24$; $p = 0.003$).

DISCUSSION

This research investigated the influence of tributaries on mainstem channel geomorphology. Based on the Network Dynamics Hypothesis, we predicted that the likelihood of a tributary to affect mainstem geomorphology would increase with the ratio of the tributary basin area to the mainstem basin area ($T_{BA}:M_{BA}$). Therefore, we expected that alluvial shoals would be more likely to occur as $T_{BA}:M_{BA}$ or T_{BA} increased. However, the distribution of alluvial shoals showed no relationship to either $T_{BA}:M_{BA}$ or T_{BA} . We did find, however, that tributaries contribute to geomorphic heterogeneity in the mainstem. In the lower river segment, alluvial shoals were closer to confluences. Additionally, throughout both river segments, shoals below large confluences were wider, had higher proportions of gravel-cobble, and less bedrock than the nearest downstream non-confluence shoal. They were also wider than downstream shoals of similar sediment composition.

This research supports the hypothesis that tributaries contribute to the formation of alluvial shoals. In the lower river segment, alluvial shoals were significantly closer to tributary confluences than other shoal clusters or equidistantly spaced points, indicating an association with tributaries. This relationship was not significant in the upper river, as naturally high

channel gradients are less conducive to the accumulation of coarse-grained alluvium.

Additionally, the pervasiveness of bedrock in the upper river segment probably contributed to the close proximity of bedrock shoals to tributary confluences in the upper river.

Large tributaries contribute to river channel geomorphic heterogeneity by influencing the sediment composition and width of shoals associated with their confluences. In the Etowah River, confluence-associated shoals had more gravel-cobble than adjacent non-confluence shoals and were wider than downstream shoals. The higher proportion of gravel-cobble may be attributed to coarse sediment delivery from tributaries and/or increased coarse sediment deposition in wider reaches with lower transport capacity compared to neighboring shoals. This geomorphic variability is likely to be ecologically significant. *Podostemum ceratophyllum* occurrence increases as both channel width and sediment size increase (Chapter 2). Because both sediment composition and *P. ceratophyllum* can influence insect (Willats 1998, Grubaugh and Wallace 1995, Argentina 2006) and fish (Freeman et al. 2003, Argentina 2006, Hagler 2006) distribution and abundance, recognizing confluence-associated shoals as unique shoal types may aid researchers in understanding the distribution patterns of aquatic organisms.

$T_{BA}:M_{BA}$ did not predict shoal occurrence below confluences (i.e., confluence effects) as was expected from the Network Dynamics Hypothesis (Benda et al. 2004a), even though the range of $T_{BA}:M_{BA}$ ratios examined here (0.0009-0.27) is within the range of ratios for humid alluvial confluences (~0.0002-0.3) included in the Benda et al. (2004a, 2004b) analysis. However, Benda et al. also reported that only 10-20% of tributary basins that were $< 1 \text{ km}^2$ affected geomorphology of river channels $> 50 \text{ km}^2$. In this study, 58% of tributary basin areas were $< 1 \text{ km}^2$, and 20% of those had alluvial shoals $< 200 \text{ m}$ downstream. Therefore, results from this study concur with those of Benda et al. (2004a); small tributaries have a low

probability of affecting river geomorphology. However, even when tributaries $< 1 \text{ km}^2$ were excluded from the analysis, $T_{BA}:M_{BA}$ ratios did not predict shoal occurrence.

The existence of a confluence effect is largely dependent upon a tributary's ability to transport sediment (Rice et al. 2006). Sediment transport is a function of tributary slope, geology (influencing both sediment supply and size), and discharge. The geology of tributary confluences with and without downstream shoals consisted of medium to high grade gneiss and schist, but limited geologic detail for most tributaries inhibited comparisons between tributaries with and without downstream shoals (Appendix E). Although we did not evaluate discharge in each of the 11 largest $T_{BA}:M_{BA}$ tributaries, we hypothesized that the presence or absence of shoals below the largest tributaries could be explained by tributary slope and sediment size. However, tributary slope and sediment size did not predict alluvial shoal presence versus absence, partly because fine sediment dominated most tributaries. The dominance of fine sediment in most tributaries is likely a consequence of historic or current agricultural land use. The shoals below channel confluences may be persistent features of the riverine landscape that reflect the historic contribution of tributary coarse sediment delivery rather than current conditions.

It is equally plausible that historic river and tributary channel modification has interrupted sediment dynamics. During subsequent field surveys, residents along the river indicated that the lower river segment was dredged in the early 1900's. Although a thorough examination of historic channelization was not conducted throughout the study area, satellite imagery and field observations indicated that one site on the mainstem and two tributaries showed evidence of channelization. Channelization functionally increases stream slope and transport capacity, resulting in upstream degradation and downstream aggradation, thus altering

the natural riffle/shoal pool sequence (Knighton 1998) and potentially reducing the propensity of tributaries to alter mainstem morphology. Therefore, historic channel modifications may have impaired the ability of tributaries to form and maintain shoals.

Although $T_{BA}:M_{BA}$ did not predict the probability of alluvial shoal occurrence below confluences, the Network Dynamics Hypothesis was supported in that shoals below large confluences contributed to riverine geomorphic heterogeneity. The higher proportions of gravel-cobble sediments and wider channels below confluences is likely to affect the occurrence of *P. ceratophyllum* (Chapters 2 and 3) and to have consequences that impact multiple trophic levels, including imperiled fishes.

IMPLICATIONS FOR PRACTICE

- Shoals associated with large tributary confluences are geomorphically different from adjacent downstream shoals. They may also be ecologically different. Recognizing confluence-associated shoals as unique shoal types may aid researchers in understanding the distribution patterns of aquatic organisms.
- Management actions that reduce the transport and deposition of coarse sediments into shoals (e.g. impoundments, flow alteration) from tributary and mainstem sources may affect the long-term persistence of alluvial shoals.

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Table 4.1. Numbers of shoals in the high bedrock, high alluvium, and moderate alluvium/moderate bedrock shoal clusters. Data were separated by upper (higher channel slope) and lower (lower channel slope) river segments.

	Upper river segment	Lower river segment
High bedrock	54	14
High alluvium	38	61
Moderate alluvium/ moderate bedrock	21	28

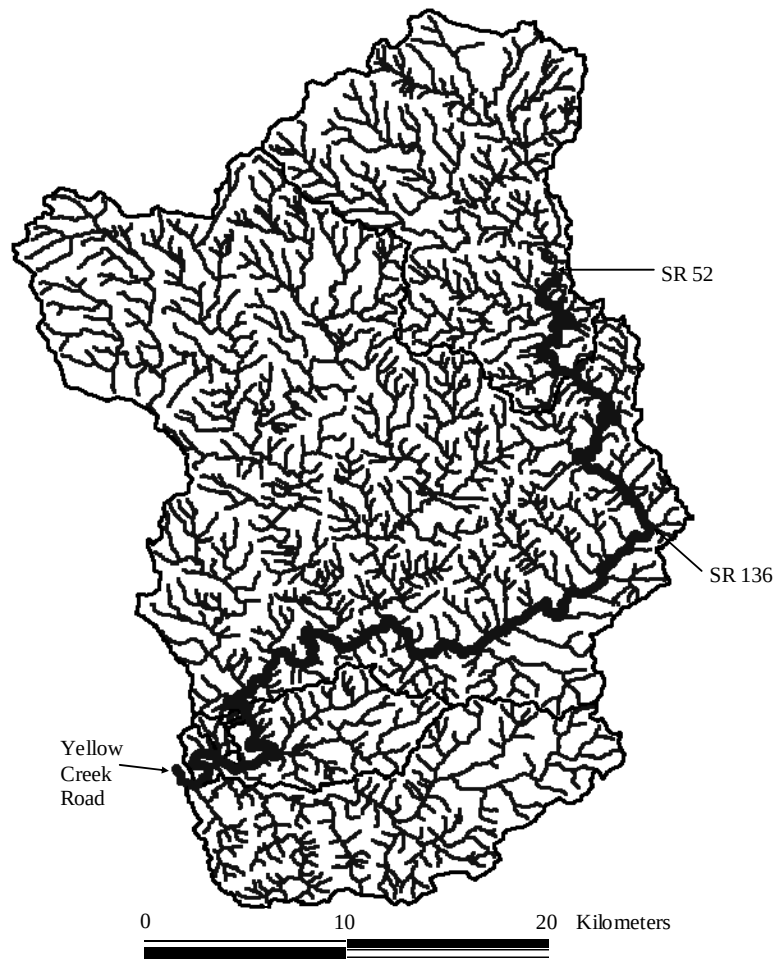


Figure 4.1. Map of the upper Etowah River watershed. Thin lines represent tributaries to the Etowah River (bold line). State Route (SR) 136 separates the upper (higher channel slope) and lower (lower channel slope) river segments.

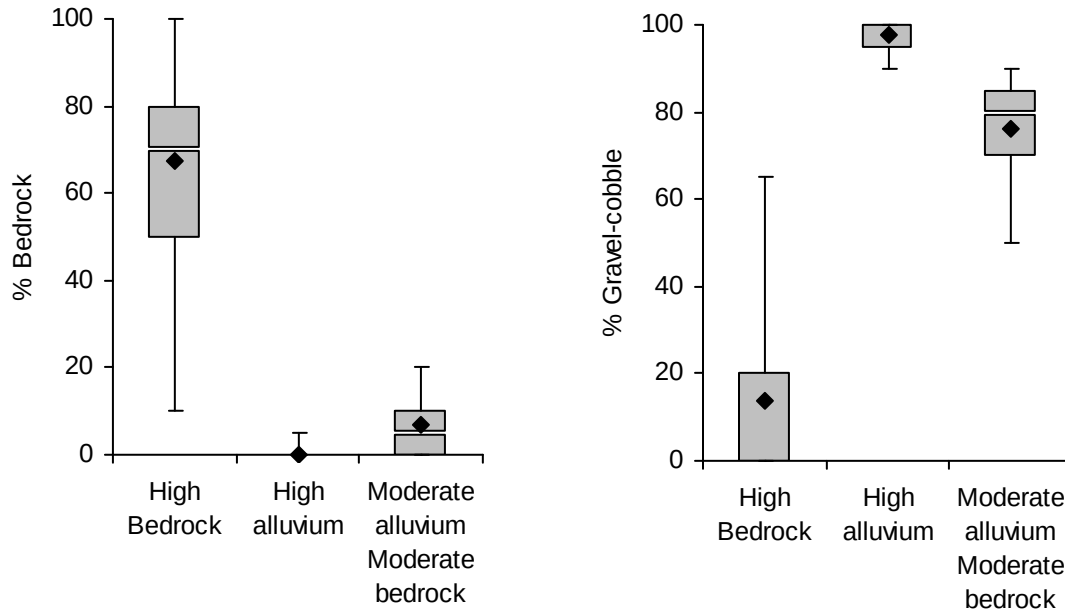


Figure 4.2. Boxplots showing A) % bedrock and B) % gravel-cobble for 3 shoal types: high bedrock, high alluvium, and moderate alluvium/moderate bedrock shoal clusters. The top and bottom points in each plot are the maximum and minimum values respectively. The tops and bottoms of the boxes are the lower and upper quartiles for each shoal type. The diamond within each box represents the median. Shoals (n = 216) were visually surveyed along 72 km of the Etowah River (Georgia, USA)

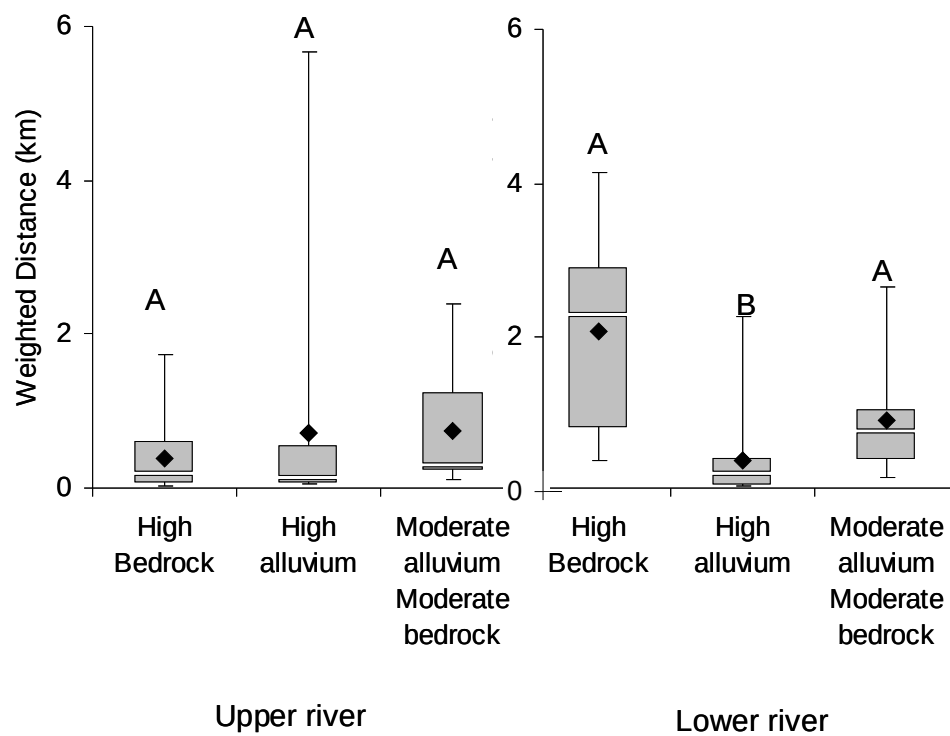


Figure 4.3. Boxplots comparing weighted distances from confluences to shoals in different clusters in the A) upper river segment and B) lower river segment of the Etowah River. The top and bottom points in each plot are the maximum and minimum values respectively. The tops and bottoms of the boxes are the lower and upper quartiles for shoal type. The diamond within each box represents the median. Different letters above plots indicate significant differences among shoal types.

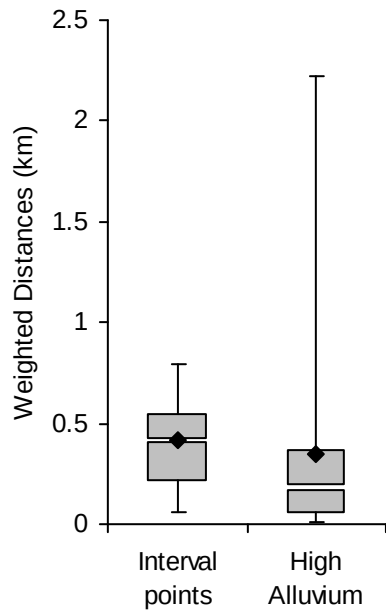


Figure 4.4. Boxplots comparing weighted distances between tributary confluences and high alluvium shoals and between tributary confluences and an equal number of equidistantly spaced points ($n = 61$) in the lower river segment of the Etowah River (Georgia, USA). The top and bottom points in each plot are the maximum and minimum values respectively. The tops and bottoms of the boxes are the lower and upper quartiles for shoal type. The diamond within each box represents the median.

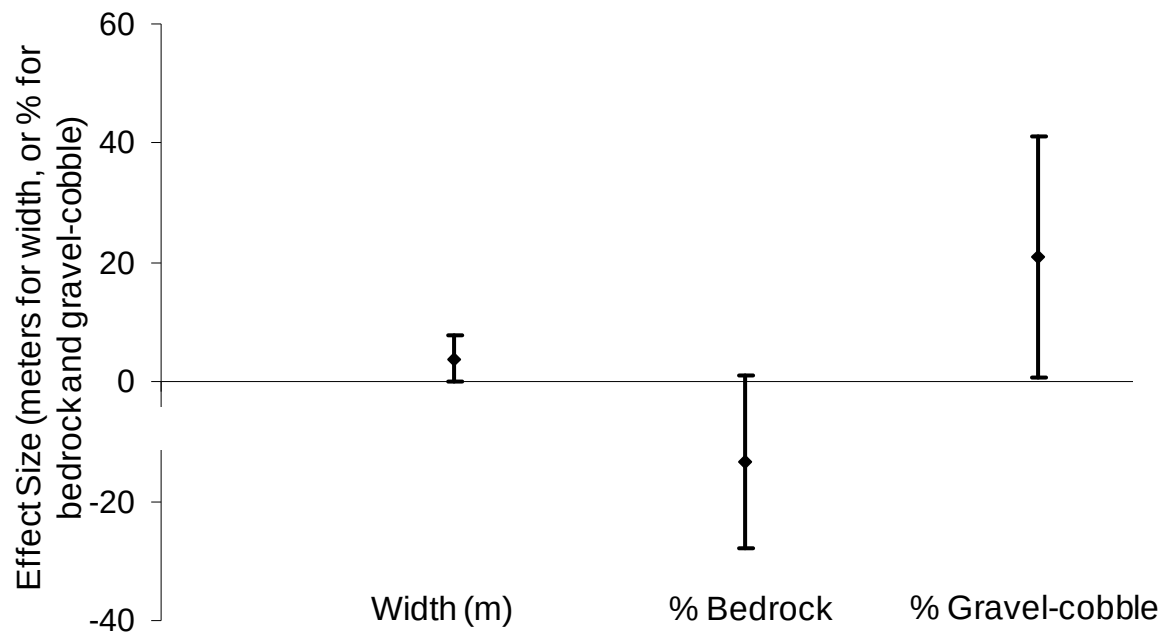


Figure 4.5. Estimates of effect size and associated 90% confidence intervals for three geomorphic attributes of confluence-associated shoals (n=6) and the nearest shoal that is downstream from the confluence-associated shoal (n=6). Effect sizes were calculated by subtracting nearest downstream shoal values from confluence-associated shoal values. Thus, a positive effect size indicates that confluence-associated shoals were wider or that they contained more bedrock or gravel-cobble than the nearest downstream shoal.

CHAPTER 5

THE INFLUENCE OF INTERANNUAL FLOW VARIABILITY ON A SOUTHEASTERN
AQUATIC MACROPHYTE⁴

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ABSTRACT

Stream flow variability is an important driver in stream ecosystems, yet its effects on ecologically important aquatic macrophytes are not well understood. The occurrence of wet, dry, and extremely dry water years between 2004 and 2007 in the Etowah River, Georgia provided an opportunity to examine the effects of flow variation on *Podostemum ceratophyllum*, an aquatic macrophyte of critical ecological importance. Monthly and annual monitoring indicated significant seasonal and interannual variability in *P. ceratophyllum* biomass, occurrence, and length. Monthly monitoring indicated that *P. ceratophyllum* biomass was highest in late summer and lowest during winter and following desiccation induced by low discharge. With the exception of the *P. ceratophyllum* desiccation period, biomass increased as discharge, depth, and velocity decreased. Among years, *P. ceratophyllum* presence and length decreased as cumulative precipitation, minimum flow, average flow, median flow, and number of peak flow days (represented by a Principal Component) increased, with minimum flow having the strongest affect on *P. ceratophyllum* presence. Because water temperatures were negatively correlated with average and median stream flow, the effects of flow on *P. ceratophyllum* may be mediated by water temperature changes. These results are particularly interesting in the context of increased water abstraction for human consumption, climate change, and instream flow management. In the absence of nutrient enrichment, reductions in growing season stream flows may cause an increase in the occurrence and length of this aquatic macrophyte, although effects of concurrent changes in temperature and land use must also be considered. However, reduced stream flows over prolonged periods may be a stressor to *P. ceratophyllum*, especially if low flows are coincident with waste-water inputs and increased algal growth.

INTRODUCTION

Stream flow variability has long been recognized as an important driver of stream ecosystems (Resh et al. 1988, Poff et al. 1997); but only recently has natural stream flow variability been studied and promoted within a management context (Richter et al. 1997). Naturally dynamic flow regimes maintain stream and river geomorphic character (Wolman and Miller, 1960, Leopold et al. 1964;) and facilitate completion of life cycles that require a diversity of flows and habitat types (Poff et al. 1997). Although a dynamic flow regime is a natural component of most free-flowing streams and rivers, extreme events such as droughts and floods may constitute disturbances to aquatic communities and populations (Resh et al. 1988). These flow extremes directly affect periphyton diversity and biomass (Clausen and Biggs 1997; Dewson et al. 2007), invertebrate community composition and abundance (Clausen and Biggs 1997; Dewson et al. 2007), and fish populations (Scheidegger and Bain 1995, Freeman et al. 2001).

Knowledge of the effects of flow variability on lotic macrophytes is important given their roles in stream ecosystems. Macrophytes produce oxygen through photosynthesis (Wilcock et al. 1999), stabilize streambed sediments by facilitating fine sediment deposition (Fritz et al. 2004), create microhabitats that are essential for stream fishes (Freeman et al. 2003), and provide unique structure on which macroinvertebrates and periphyton occur (Grubaugh and Wallace 1995, Willats 1998).

Flow affects aquatic organisms directly (e.g., water depth and velocity) and indirectly by affecting the physicochemical characteristics of water (e.g., temperature variation and nitrate concentration; Poff et al. 1997). The frequency of high-flow events is thought to directly affect lotic aquatic macrophyte distribution, but between flood spates in stable systems, distribution is

strongly influenced by local hydraulic and geomorphic conditions (Chapters 2 and 3; Riis and Biggs, 2003). However, in groundwater-fed streams affected by drought, the relative permanence of water is an important determinant of macrophyte community composition (Westwood et al. 2006a). Additionally, land use in combination with water abstraction from headwater chalk streams influences macrophyte community composition (Westwood et al. 2006b). Although these studies highlight the importance of water quantity and quality on stream macrophytes, further research on the effects of flow variability on macrophytes is needed.

We expect that lotic macrophytes are extremely responsive to flow variability and associated water quality changes, even in the absence of complete stream dewatering or extremely large floods. For example, during drought, water temperature generally increases as flow decreases (Cowx et al. 1984). However, depending on the groundwater contribution to stream flow, water temperature may also decrease (Grant 1977, Mosley 1983). Temperature changes alter plant physiology, distribution, and nutrient uptake (Lambers et al. 1998). In addition to changes in temperature, dry periods may be characterized by lower stream nutrient levels because of reduced runoff (Caruso 2002) and increased groundwater contribution to stream flow (Dahm et al. 2003). Alternatively, in streams receiving wastewater effluent, elevated nutrient concentrations are likely. Altered nutrient concentrations can have substantial effects on plant growth (Cushing and Allan 2001; Hillebrand 2002). Given the important ecological roles of aquatic macrophytes and their potential susceptibility to water quality and quantity changes, we would expect additional ecological consequences should flow-induced changes in plant occurrence occur.

Climate change, increased water allocation for consumptive use, and flow regulation by dams have placed increased demands on streams and rivers (Palmer et al. 2008), resulting in the

alteration of natural stream flow variation (Richter et al. 1997). Understanding aquatic ecosystem responses to altered stream flows and to stream flow variability will inform the management of aquatic ecosystems.

The wet, dry, and extremely dry water years from 2004-2007 provided an opportunity to examine the effects of stream flow variation on an aquatic macrophyte, *Podostemum ceratophyllum*. *P. ceratophyllum* (riverweed) Michx. was chosen as the study organism because it is the dominant lotic macrophyte in the southeastern United States, it has a strong influence on the occurrence of fishes (Connelly et al. 1999, Freeman et al. 2003, Argentina 2006, Hagler 2006), and the effects of flow variability on its distribution and growth were unknown. Specifically, we asked whether river discharge, precipitation, and local geomorphic variables explain a significant portion of the interannual variation in *P. ceratophyllum* presence, length, and biomass. We also assessed whether the effects of discharge on *P. ceratophyllum* are mediated by water temperature and changes in nitrate concentration.

Study system

This research took place in shoals of the upper Etowah River, a 5th to 6th order north Georgia U.S.A. river that drains the Southern Blue Ridge and Piedmont physiographic provinces. The Etowah River above Yellow Creek Road and below State Route 136 (48 km) was selected as the study reach because it is designated as high priority for restoration and preservation by USFWS (Freeman and Wenger 2000), is of relatively uniform gradient, and is dominated by alluvial processes. A humid climate with average annual rainfall between 147 and 178 cm characterizes this region of Georgia (NOAA 2008). Precipitation maxima (10-15 cm per month) associated with frontal systems occurs in the spring, but summer thunderstorms may also produce large

rainfall quantities (10- 18 cm per month; NOAA 2008). Measurable rainfall occurs on average 120 days out of the year, resulting in frequent increases and decreases in the river hydrograph (Figure 5.1; NOAA 2008). Average monthly discharge is typically highest in March and lowest in September and October (NOAA 2008).

Shoals are shallow parts of river channels (USDA 2003), generally with higher gradients than surrounding channel units. *Podostemum ceratophyllum* (riverweed) Michx. is the dominant lotic macrophyte in rocky shoals of the southeastern United States. Both *P. ceratophyllum* occurrence and length increase as sediment size increases (Chapter 3). In the Etowah and Conasauga rivers, benthic imperiled fishes are more likely to occur in the presence of *P. ceratophyllum* (Freeman et al. 2003, Argentina 2006, Hagler 2006). *P. ceratophyllum* is also a critical structural habitat component for the endemic Etowah caddisfly (Willats 1998), as well as increasing surface area 3-4 times over bare rock (Hutchens et al. 2004), facilitating high total macroinvertebrate biomass and abundance (Grubaugh and Wallace 1995, Grubaugh et al. 1997, Hutchens et al. 2004, Argentina 2006).

METHODS

P. ceratophyllum monitoring

We assessed *Podostemum ceratophyllum* response to seasonal and interannual stream flow variation in the Etowah River, GA in two ways: by monitoring biomass monthly on a shallow bedrock outcrop and by annual sampling. Monthly monitoring took place along a single 18m bedrock outcrop (34° 21' 42.40" N, 84° 11' 12.51"W) from April 2006 to October 2007 (n = 19 months). The site was chosen because it was accessible by foot and was on public land (Dawson Forest). At 10 random locations along the bedrock outcrop, water depth and velocity were

measured. A 180 cm² subsection of a Surber sampler was placed at each location along the outcrop and *P. ceratophyllum* was manually removed by hand until all that remained were the firmly attached roots. Samples were preserved in 70% ethanol, separated from other organic matter, and dried at 50°C in a drying oven. Because *P. ceratophyllum* dry mass predicts ash free dry mass ($R^2=0.98$, $p<0.001$, Appendix F), we used dry mass as our biomass estimate.

Annual sampling was conducted at 11 sites between 27 July – and 15 October in 2004-2007 (Figure 5.1, Appendix G, $n = 4$ years), with sampling times corresponding to the peak of the *Podostemum ceratophyllum* growing season. Sites were chosen based on accessibility, but all were dispersed throughout the river segment by selecting sites above and below third order tributaries.

Upstream and downstream shoal boundaries were marked to ensure repeated sampling of the same area. Wolman pebble counts were used to measure sediment particles on a minimum of 100 sediments per shoal (Wolman 1954) and were conducted each year along 10-12 transects equidistantly spaced to span the entire shoal length. Sediment measurements were grouped in size classes that increase by powers of 2 (Wentworth 1926).

Each particle collected in the pebble count ($n = 5533$) was visually assessed for the presence of *P. ceratophyllum*. Because of the large number of plant stems on a particle and the impracticality of measuring multiple stems or biomass, maximum plant length (a biomass correlate, Appendix D) was recorded as a standardized plant quality measurement repeatable among observers. Only samples in which *P. ceratophyllum* was present ($n=1118$) were included in the analysis of discharge, precipitation, and sediment effects on plant length.

Discharge, Temperature, and Nitrate

Discharge in the Etowah River was compared to long-term average and minimum monthly flow data using a USGS streamflow gage (USGS gage # 02392000) with 80 years of record and located 51 river kilometers downstream from the lowermost sample site. To examine the effects of interannual flow variability on *P. ceratophyllum* presence and length, average daily discharge data from a nearby USGS gage (USGS gage 02389150; period of record 2003-present) on the Etowah River were used. All sites were within 28 river kilometers of the USGS gage.

Data from the USGS gage were used to calculate total precipitation, maximum, minimum, average, median, and number of peak flows from January until the date of sample collection (Table 5.1; Figure 5.1), as this period encompassed the growing season and is the time period most likely to affect plant growth (Figure 5.2). Because of the limited period of record at the gage, recurrence interval flow statistics could not be used to define peak flows. Thus, the number of days with peak flows exceeding 500 cubic feet per second (cfs) was used as an indicator of high flow conditions, as this was the flow above which hydrograph spikes were evident (Figure 5.1).

To examine relationships between discharge, water temperature, and nitrate concentrations ($\text{NO}_3 + \text{NO}_2\text{-N}$), temperature and nitrate data were obtained from USGS gage 02392000. Because temperature and nitrate data were collected sporadically at the gage site, only average monthly values were available from April to August, 2004-2007. Minimum, maximum, average, median flow, and number of peak flow days were derived from January until the median *P. ceratophyllum* sample date.

Statistical Analysis

Average monthly *P. ceratophyllum* biomass on the bedrock outcrop was compared to average depth and velocity using correlation analysis. Correlation analysis was also used to relate average biomass to average, median, and minimum discharge 30 days prior to the sample collection date.

Two analyses were used to test for effects of hydrology on *P. ceratophyllum* occurrence and length, the first used individual flow variables and the second used principal components to represent all flow variables. The first analysis used simple linear regression to identify precipitation and hydrologic variables that affected average *P. ceratophyllum* occurrence (proportion of rocks with riverweed) and length among all sites. Variables with statistically significant R^2 values were retained in a logistic regression analysis for effects on *P. ceratophyllum* presence, and in a mixed model analysis for effects on length (described below).

Because total precipitation, maximum, minimum, average, median, and number of peak flows are correlated, a second analysis used principal components to represent these variables. This technique reduces multidimensional data sets to lower dimensions for further analysis. Principal components were calculated in PC-ORD software (McCune and Mefford 1999). *P. ceratophyllum* presence and length data sets differed greatly in sample size ($n = 5533$ and 1118 , respectively), and therefore, separate flow principal components were developed for each parameter (Table 5.2). Only components with eigen values >1 were selected to represent flow variables.

Because sediment size is an important predictor of *P. ceratophyllum* occurrence and length (Chapter 3), it was included in both logistic regression and mixed model analyses.

Generalized estimating equations for repeated measured analysis in PROC GENMOD (Littell et al. 2002; SAS Institute, Cary, NC) were used to test 1) the effect of individual flow variables and sediment size on *P. ceratophyllum* presence, and 2) the effects of flow principal components and sediment size on *P. ceratophyllum* presence. Parameter estimates, chi-square statistics, and p-values were calculated using the BINOMIAL option in PROC GENMOD, used for dichotomous response variables with binomial distributions (Allison 1991). A repeated component was included to account for the repeated annual sampling of sites, with sites nested within years.

PROC MIXED was used to evaluate 1) the effects of individual flow variables and sediment size on *P. ceratophyllum* length and 2) the effects of flow principal components and sediment size on length. A repeated component was included to account for the repeated annual sampling of sites, with sites nested within years. It was necessary to log-transform sediment size data for the *P. ceratophyllum* length analysis, but not the presence analysis. *P. ceratophyllum* length data were square-root transformed. An *a priori* p-value of $p < 0.10$ was selected as the threshold for statistical significance (*sensu* Johnson 1999).

To assess potential mechanisms through which flow affects *P. ceratophyllum*, a correlation matrix was used to assess relationships among discharge, temperature, and nitrate variables.

RESULTS

Seasonal Variation

Monthly monitoring along the bedrock outcrop indicated significant seasonal and interannual variability (Figure 5.2). Extremely cold water temperatures prevented adequate sampling in January and February of 2007; however, visual observations indicated that the plant

senesced during these months as it had done in 2006. Low biomass was also observed in September 2007 when low discharge and shallow water depths exposed the bedrock outcrop and *P. ceratophyllum* to the air and caused plant desiccation (Figure 5.2). Peak biomass was from August-October in 2006 and June-August in 2007.

Average monthly biomass was not correlated with average, median, or minimum discharge for 30 days prior to the sample date ($R = -0.23$ $p = 0.38$, $R = -0.24$ $p = 0.35$, and $R = -0.28$ $p = 0.28$, respectively). Average monthly biomass was not correlated with average water depth or velocity ($R = -0.03$ $p = 0.91$, $R = -0.16$ $p = 0.53$, respectively). Excluding the September and October 2007 measurements (i.e., the period of *P. ceratophyllum* desiccation induced by extremely low flows), average monthly biomass was negatively correlated with average, median, and minimum (Figure 5.3a) discharge ($R = -0.63$ $p = 0.01$, $R = -0.71$ $p = 0.003$, and $R = -0.72$ $p = 0.002$, respectively) and with average water depth (Figure 5.3b) and velocity ($R = -0.57$ $p = 0.03$, $R = -0.64$ $p = 0.01$, respectively).

Interannual Variation of *P. ceratophyllum* Presence

Average discharge spanned wet (2005), dry (2004 and 2006), and extremely dry (2007) water years (Figure 5.4a). Prior to the sample period (January to August), average and minimum discharge were above the long-term average in 2005 and below the long-term average in 2004 and 2006. Minimum discharge was lowest in 2007 (Table 5.1), and was 78% lower than the long-term average minimum discharge for August (Figure 5.4b).

Simple linear regression analysis indicated that the average proportion of sediments with *P. ceratophyllum* decreased as minimum flow in the growing season prior to the sample date increased ($R^2 = 0.83$, $F_{1,3} = 9.4$, $p = 0.09$; Figure 5.5). All other flow and precipitation variables in

the simple linear regression analysis were not significant. Cumulative precipitation, minimum, average, median, and number of peak flow days were negatively correlated with Principal Component (PC) 1, and maximum flow was negatively correlated with PC2 (Table 5.2).

Using both minimum flow and sediment size to predict *P. ceratophyllum* presence, *P. ceratophyllum* was more likely to be present as sediment size increased (Appendix H, $X^2_{(1)}=3.6$, $p=0.057$), and less likely to be present as minimum flow increased ($X^2_{(1)}=5.3$, $p=0.02$). The effect of minimum flow on *P. ceratophyllum* presence did not depend upon sediment size (minimum flow*sediment size; $X^2_{(1)}=0.18$, $p=0.67$).

When flow principal components and sediment size were tested for effects on *P. ceratophyllum* presence, *P. ceratophyllum* was more likely to be present as sediment size increased ($X^2_{(1)}=6.1$, $p=0.01$). *P. ceratophyllum* was more likely to be present as PC1 increased ($X^2_{(1)}=6.2$, $p=0.01$), indicating that presence decreased as precipitation, minimum flow, average flow, median flow, and number of peak flow days increased. There was no effect of PC2 ($X^2_{(1)}=1.4$, $p=0.24$), indicating that maximum flow had little effect. Furthermore, there were no significant interactions (PC1*sediment size, $X^2_{(1)}=1.3$, $p=0.26$; PC2*sediment size $X^2_{(1)}=2.6$, $p=0.11$), indicating that the effects of PC1 and PC2 did not depend on sediment size.

Average and median discharge, and the number of peak flow days were negatively correlated with temperature in July ($p < 0.05$). Minimum flow was positively correlated with nitrate concentration in July, and median flow was positively correlated with nitrate concentration in June ($p < 0.05$; Appendix I).

Interannual *P. ceratophyllum* length

Simple linear regression analysis indicated that average *P. ceratophyllum* length among all sites increased as maximum flow prior to sample date increased ($R^2 = 0.87$, $F_{1,3}=12.8$, $p=0.07$; Figure 5.6). All other precipitation and flow variables in the simple linear regression analysis were not significant. Cumulative precipitation, minimum, average, median, and number of peak flow days were negatively correlated with PC1, and maximum flow was negatively correlated with PC2 (Table 5.2).

P. ceratophyllum length increased significantly with particle size ($F_{1,41}=5.27$, $p=0.03$), but showed no change with either maximum flow ($F_{1,1031}=0.0$, $p=0.99$) or the maximum flow*sediment size interaction ($F_{1,1031}=0.67$, $p=0.41$). When sediment size and both principal components (representing flow) were tested, *P. ceratophyllum* length increased with sediment size ($F_{1,1112} = 130.70$; $p < 0.0001$) and with PC1 ($F_{1,1112}=3.05$; $p=0.08$), indicating that length decreased as cumulative precipitation, minimum flow, average flow, median flow, and number of peak flow days increased. There was no significant change in *P. ceratophyllum* length with PC2 ($F_{1,1112}=0.00$; $p=0.95$) or with the interaction terms (PC1*sediment size $F_{1,1112}=1.62$; $p=0.20$; PC2*sediment size $F_{1,1112}=0.57$; $p=0.45$).

DISCUSSION

These results highlight the influence of stream flow variability on an aquatic macrophyte. Although large floods reduce *P. ceratophyllum* occurrence and length (Chapter 2), these data indicate that interannual stream flow variation affects *P. ceratophyllum* even in the absence of large floods. Additionally, the findings that sediment size is a primary determinant of *P. ceratophyllum* occurrence among sites and that extremely low water depths decrease *P.*

ceratophyllum biomass support previous studies (Chapters 2 and 3, Nelson and Scott 1962, Argentina 2006).

Biomass measurements on the bedrock outcrop were lower compared to other studies of *P. ceratophyllum* biomass on bedrock outcrops in other drainages (Appendix J; Nelson and Scott 1962, Grubaugh and Wallace 1995, Grubaugh 1997, Hutchens et al. 2004). However, stream order and basin area were also smaller compared to other studies (Appendix J). Because *P. ceratophyllum* length (a biomass correlate; Chapter 3) increases with increasing basin area, the low biomass observed in our study site may be a function of the site's position within the drainage.

P. ceratophyllum biomass on the bedrock outcrop varied seasonally, with peaks in mid-late summer. Biomass increased as average, median, and minimum flows decreased, and as water depth and velocity decreased. However, biomass differed greatly in September 2006 and 2007, highlighting the effects of very low flows in 2007 on slightly submerged macrophytes. While *P. ceratophyllum* desiccated on the bedrock outcrop, occurrence among sites was highest in 2007, indicating that water depth also plays an important role in the persistence of this species. Therefore, reduced discharge, depth, and velocity may subsidize plant growth but may stress plants when discharge reductions cause plant desiccation.

P. ceratophyllum presence and length decreased as cumulative precipitation, minimum flow, average flow, median flow, and number of peak flow days (represented by a Principal Component) increased, with minimum flow having the strongest affect on *P. ceratophyllum* presence. These data indicate that even in the absence of flow cessation, a significant portion of the interannual variation in macrophyte occurrence can be accounted for by minimum instream flow. However, these results may have been different had the Etowah River been nutrient

enriched by waste-water or other sources. In the nutrient enriched Middle Oconee River, Georgia, dense layers of filamentous algae covered *P. ceratophyllum* in bedrock shoals during the same period. The authors speculate that increased algae may reduce light availability and impair macrophyte growth, but additional research is needed to assess macrophyte responses to nutrient enrichment and algal growth.

Although average macrophyte length increased as maximum flow increased among all sites in the simple linear regression, it had no effect when included in analyses that accounted for site-level variation, sediment size, or when it was represented by a Principal Component. Flood flows associated with Hurricane Ivan decreased *P. ceratophyllum* length in a separate study (Chapter 2), and we may have detected a stronger effect of maximum flows on both macrophyte presence and length had the analysis encompassed a larger range of maximum flows. Among year variation in maximum flow was insufficient to affect *P. ceratophyllum* differently during the 4 years of our study, and therefore, there was no statistical effect of maximum flows on *P. ceratophyllum*.

Flow variation may have indirectly affected macrophyte occurrence and length through changes in water quality. In the absence of wastewater inputs, nutrient enrichment generally decreases during drought as a consequence of decreased runoff (Dewson et al. 2007). Reduced nutrients can cause macrophyte and periphyton biomass decreases (Cushing and Allen 2001). However, nitrate concentrations in June and July increased as median and minimum flows increased, respectively. And because *P. ceratophyllum* length and occurrence were lowest in high flow and high nitrate years, flow effects were probably not mediated by changes in nitrate concentration. However, temperature increased as average, median, and number of peak flow

days decreased, suggesting that *P. ceratophyllum* presence and length are likely to be higher in years with lower flows and higher temperatures.

Cumulative precipitation did not account for a significant portion of the among-year variation in plant presence and length, although it was highly correlated with principal component 1. However, precipitation obviously influences both minimum and maximum stream flow. Cumulative precipitation wasn't correlated with minimum or maximum flow among the 4 years studied at our site. However, at a downstream gage with a longer precipitation and flow record (6 years; USGS gage 02392000), minimum flows from January through August were positively correlated with cumulative precipitation (minimum flow: $R = 0.80$, $p = 0.05$; maximum flow: $R = 0.34$, $p = 0.51$).

Precipitation decreases are likely to reduce river discharge. Years with low discharge may result in the proliferation of *P. ceratophyllum*. However, this view of the relationships among precipitation, discharge, and *P. ceratophyllum* may be overly simplistic. Short periods of reduced discharge may subsidize plant growth, but multiple consecutive years of low discharge (i.e., originating from climate change or water abstraction) are likely to be confounded by other factors. Reduced stream flows have been associated with increased fine sediment deposition rates (see review in Dewson et al. 2007), and climate change effects are likely to be confounded by landcover changes that exacerbate bed sediment fining. Because *P. ceratophyllum* does not occur on sand and silt bed sediments (Chapter 3), climate change effects on flow may be swamped by concurrent changes in sediment size.

Instream flow management may also affect *P. ceratophyllum*. Flow prescriptions that rely on low flow statistics (e.g., 7Q10) and dam operations that decrease interannual flow variation and affect water temperature may also affect *P. ceratophyllum* presence, length, and

biomass variation. Low flow prescriptions that expose coarse sediments will likely decrease *P. ceratophyllum* biomass. Changes in *P. ceratophyllum* presence, biomass, and length are likely to affect aquatic insect larva abundance (Chapter 3) and fish occurrence (Freeman et al. 2003, Argentina 2006, Hagler 2006). However, instream flow management options that incorporate natural streamflow variation are more likely to facilitate the persistence of *P. ceratophyllum* and the species with which it is associated.

IMPLICATIONS FOR PRACTICE

- *P. ceratophyllum* is affected by streamflow. Because stream flow is likely to be affected by land use change, climate change, and water abstraction, sites should be routinely monitored to assess both short and long-term effects on *P. ceratophyllum*.
- Should nitrate concentrations increase as a consequence of land use change or increased point-sources, shoals should be routinely monitored to assess both short and long-term effects on algal growth and *P. ceratophyllum*.
- Although *P. ceratophyllum* occurrence and length increased as flows decreased during this study period, continued low flows may be a stressor to *P. ceratophyllum*. Additionally, effects of reduced flows on other ecosystem components (i.e., imperiled species, aquatic macroinvertebrates) may differ.
- Future studies of flow effects on *P. ceratophyllum* should include concurrent measurements of nutrient concentration and water temperature.
- Should long-term *P. ceratophyllum* monitoring be adopted, the effects of seasonal *P. ceratophyllum* variation can be minimized by sampling during the peak of the growing season.

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Table 5.1. Precipitation (cm) and Etowah River flow summary statistics (in cubic feet/ second, cfs) from USGS gage 02389150, from January until sample collection date. Peak flow days are defined as the number of days in which flows exceeded 500 cfs.

Year	Cumulative Precipitation	Minimum Flow	Maximum Flow	Average Flow	Median Flow	Peak flow days
2004	64	121	775	240	223	4
2005	106	181	1280	358	310	27
2006	70	66	945	197	195	4
2007	56	51	1840	223	203	11

Table 5.2. Correlation coefficients on principal components and the variables that they represent. Separate principal components were developed for the length and presence/absence analyses because of different sample sizes.

	Cumulative Precipitation	Minimum Flow	Maximum Flow	Average Flow	Median Flow	Peak flow days
Presence/Absence Analysis						
PC1	-0.90	-0.89	-0.09	-0.99	-0.99	-0.93
PC2	0.09	0.37	-0.99	-0.03	0.04	-0.36
Length Analysis						
PC1	-0.85	-0.88	-0.01	-1.00	-1.00	-0.89
PC2	0.08	0.43	-0.99	-0.04	0.05	-0.43

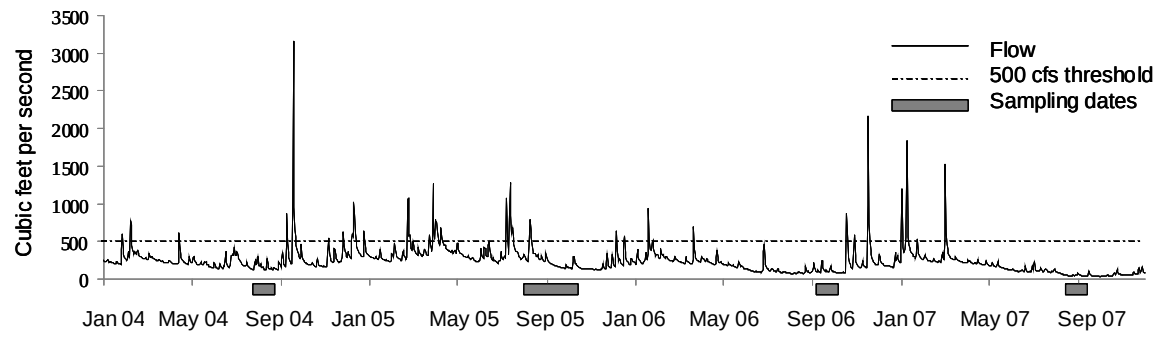


Figure 5.1. Stream flow in the Etowah River (2004-2007) at USGS gage 02389150. The line demarcating 500 cubic feet per second was the threshold above which flows were considered to be peak flows. Sampling dates are shown by the grey boxes.

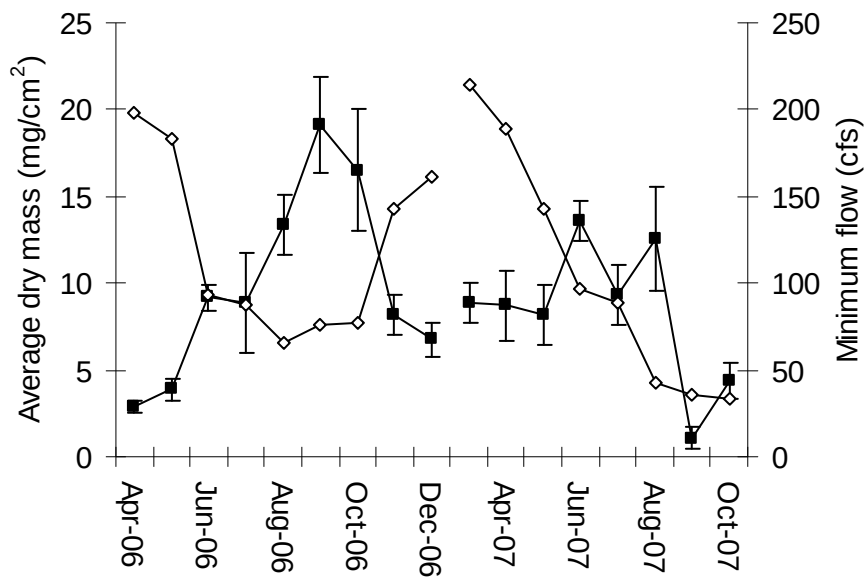


Figure 5.2. Seasonal variation in *Podostemum ceratophyllum* mass (dark squares) and A) minimum flow measured within 30 days prior to sample collection (open diamonds) along a bedrock outcrop in the Etowah River (Georgia, USA). Each dry mass point represents an average of 10 measurements $\pm$ one standard error.

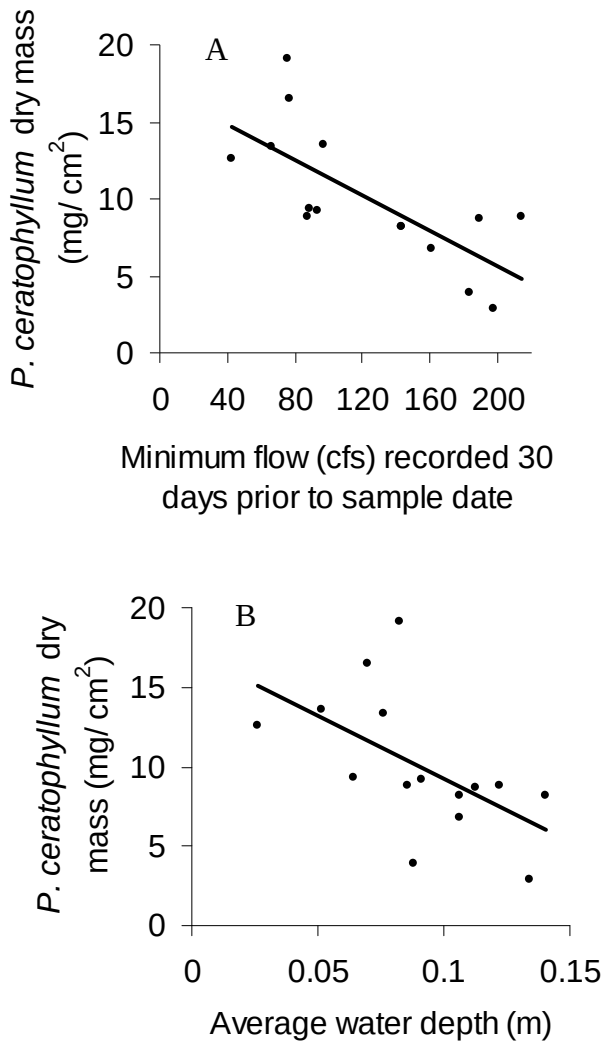


Figure 5.3. Correlation of *P. ceratophyllum* dry mass and A) average minimum flow and B) water depth along a bedrock outcrop in the Etowah River (Georgia, USA). Each point represents an average of 10 water depth and dry weight measurements.

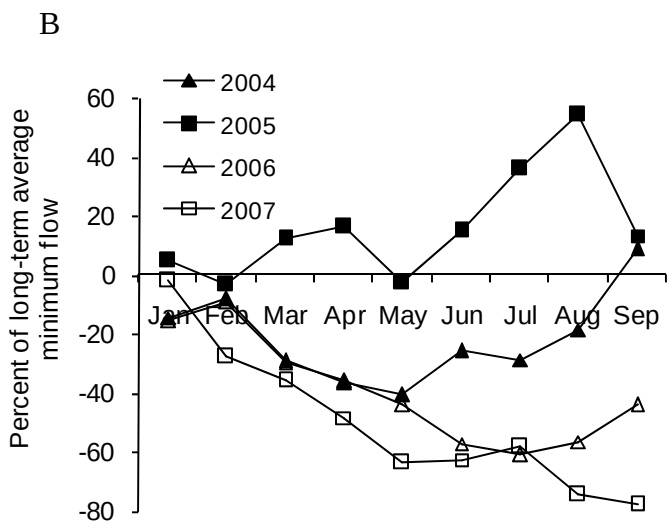
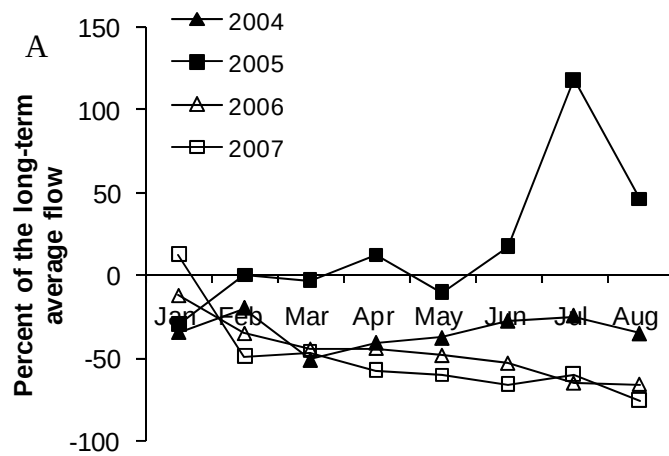


Figure 5.4. Average (A) and minimum (B) stream flow in the Etowah River from 2004-2007 expressed as a percent of the long-term average for each month.

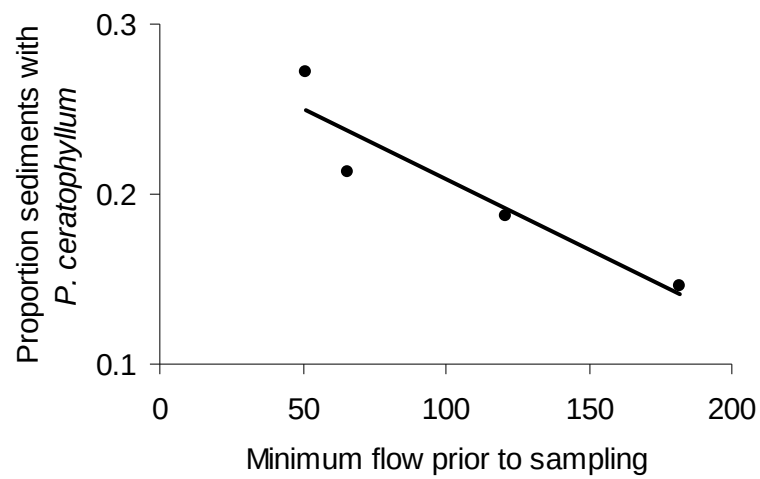


Figure 5.5. Effects of minimum flow (from January until sample collection for each year) on the proportion of sediments with *Podostemum ceratophyllum*, averaged for all sites each year.

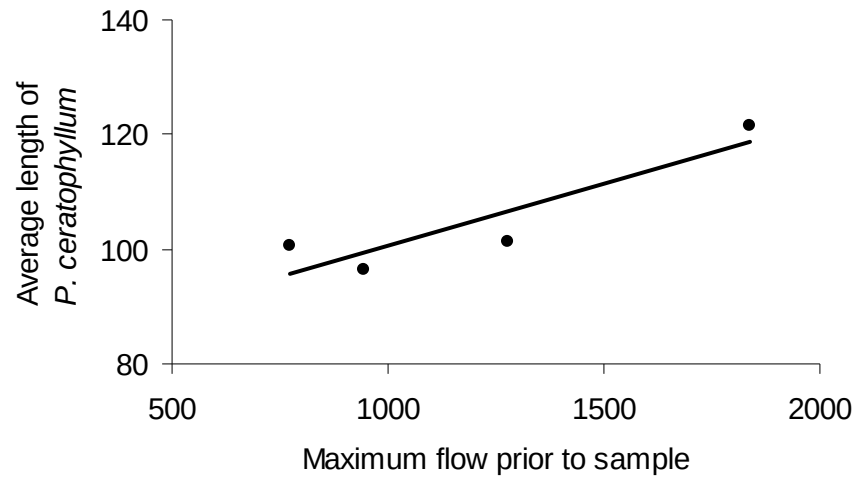


Figure 5.6. Effects of maximum flow (from January until sample collection for each year) on the average length of all *Podostemum ceratophyllum* measurements, averaged for all sites each year.

CHAPTER 6

CONCLUSIONS

Habitat management is complicated by the complexity and dynamic nature of ecosystems (Gunderson 1999), making scientific research an essential component of successful habitat management (Blockstein 1999, Haynes et al. 2001). Historic and present impacts to aquatic ecosystems have fueled a multibillion dollar effort to improve or restore aquatic ecosystems (Bernhardt et al. 2005; Palmer et al. 2005). Yet, the ecological consequences of these efforts are largely unknown (Kondolf 1995; Bernhardt et al. 2005). A scientific evaluation of potential restoration actions and likely outcomes could improve management effectiveness and inform future management efforts (Downs and Kondolf 2002).

Restoration projects that are guided by channel geomorphology may successfully improve instream habitat, as some geomorphic variables can have a strong influence on aquatic habitats and fauna (e.g. Freeman et al. 2003, Fritz and Feminella 2003, Gangloff and Feminella 2007). Thus, the objective of this dissertation was to increase scientific understanding of the hydrologic and geomorphic factors that control ecologically important instream habitats in the Etowah River, Georgia. Research questions were addressed in a manner that not only contributed to management and restoration, but also to the scientific understanding of aquatic ecosystems.

Instream habitat variables that are important to imperiled Etowah River fish include the proportion of fines, cobble, and gravel in sediments and the presence of *P. ceratophyllum*. Because incised river channels represent geomorphic degradation, I expected that these instream habitat variables would differ between incised and slightly incised shoals. Incised and slightly

incised shoals did not differ in the proportion of fines, cobble, and gravel in sediments, nor did they differ in the occurrence of *Podostemum ceratophyllum*. The lack of imperiled species habitat differences between incised and slightly incised sites is particularly interesting in the context of channel restoration for habitat improvement purposes. Incision is often used in combination with additional variables (e.g., species distribution data) to select restoration sites (Rosgen 1997). But our results suggest that important instream habitat variables did not differ between incised and slightly incised shoals, and that geomorphic degradation does not necessarily reflect habitat degradation.

However, the observation that floods, channel geometry, and sediment size were useful predictors of *P. ceratophyllum* occurrence and length illustrates the importance of shoal-scale geomorphology to instream habitat, with sediment size playing a principal role (Chapter 2). Restoration approaches that increase instream sediment size may increase *P. ceratophyllum* occurrence, length, and persistence with consequent positive impacts on imperiled species (Hagler 2006).

P. ceratophyllum occurrence increased with sediment size and channel width, whereas *P. ceratophyllum* length increased with sediment size and basin area (Chapter 3). Increases in channel width were correlated with decreased shade, and facilitated higher *P. ceratophyllum* density and *Brachycentrus etowahensis* (Etowah caddisfly) abundance. These relationships implicate sediment size and channel width as dominant geomorphic factors that control shade, primary producers, and caddisfly abundance in Etowah River shoals (Chapter 3).

Multiple factors likely control coarse sediment and channel width variation among shoals. The Network Dynamics Hypothesis (NDH) predicts that tributaries influence mainstem morphology via tributary sediment inputs. Although the ratio of tributary to mainstem basin area

did not predict shoal occurrence as predicted by the NDH, alluvial shoals were closer to confluences than shoals with bedrock in downstream reaches of the study area (Chapter 4). Shoals below large confluences were wider than downstream shoals, and had higher proportions of gravel-cobble, and less bedrock (Chapter 4). Therefore, large tributaries contribute to river channel geomorphic heterogeneity by influencing sediment composition and width of shoals associated with their confluences. Because sediment size and channel width affected *P. ceratophyllum* occurrence (Chapter 3), confluence-associated shoals likely differ from other shoals in *P. ceratophyllum* occurrence. Both sediment composition and *P. ceratophyllum* influence insect (Grubaugh and Wallace 1995, Willats 1998, Argentina 2006) and fish (Freeman et al. 2003, Argentina 2006, Hagler 2006) distributions; therefore confluence-associated shoals may also have different fish and invertebrate communities.

Hydrology and geomorphology influenced *P. ceratophyllum* within and among shoals (Chapters 2-4), but *P. ceratophyllum* presence and length also varied among years, increasing as flows from January to the summer sample date (the period of plant growth) decreased (Chapter 5). Minimum flow was the strongest hydrologic predictor of *P. ceratophyllum* presence among years (Chapter 5). Because water temperature increased as flows decreased, the effects of flow may have been mediated by water temperature changes. Monthly monitoring indicated that *P. ceratophyllum* biomass increased as discharge, depth, and velocity decreased, with biomass highest in the late summer and lowest during winter. However, very low flows exposed sediments and caused plant desiccation, indicating that the relationship between flow and *P. ceratophyllum* is probably curvilinear. Management actions that reduce flows during the growing season may increase *P. ceratophyllum* presence and length, although the effects of prolonged changes in water temperature and discharge also should be considered. Additionally,

effects of reduced flows on other ecosystem components (i.e., imperiled species, aquatic macroinvertebrates) may differ.

This research enhances scientific understanding of the relationships between hydrology, geomorphology and habitats of imperiled fishes in the Etowah River, GA. This knowledge may help guide management efforts directed at improving imperiled fish habitats. However, much remains to be investigated regarding geomorphic, hydrologic, and ecological linkages. Several questions that stem from this research merit further investigation including: 1) Is the Etowah River unique with regards to the lack of a relationship between channel entrenchment and instream habitat? 2) Do confluence-associated shoals harbor more *P. ceratophyllum* than non-confluence shoals as predicted, and do these habitat differences account for variation in imperiled fish occurrence? 3) How will climate change affect spring and summer stream flows, and how will these flow changes interact with other factors (e.g., changing temperature, land use) to affect *P. ceratophyllum* over longer periods? and 4) How do flow alterations (e.g. higher baseflows, lower peak flows, flashy hydrology), and altered sediment composition caused by hydropower management affect *P. ceratophyllum*?

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APPENDIX

Appendix A: Summary statistics describing geomorphology and *Podostemum ceratophyllum* for sites sampled in 2004 in the Etowah River.

Appendix B: Relationship between shoal basin area and estimated percent bedrock from the visual survey in 2005 (n=216).

Appendix C: Representation of the modified channel cross-section method and measurement steps. A) Visual estimates of x,y coordinates (red dots) at major bank slope changes were combined with water depth measurements (red dots) at major changes in bed slope to produce B) channel cross sections.

Appendix D: Relationship between *P. ceratophyllum* maximum length and ash free dry mass per cm² (n = 57).

Appendix E. Lithology of 11 tributaries with the largest tributary basin area to mainstem basin area ratios. All geologic data presented here are derived from German (1985), The Geology of the Northeastern Portion of the Dahlonga Gold Belt.

Appendix F: Regression of *Podostemum ceratophyllum* ash free dry mass (AFDM) on *P. ceratophyllum* dry mass. Samples were collected from a 180 cm² subsection of a Surber sampler on a bedrock outcrop in the Etowah River in Dawson Forest, Georgia.

Appendix G: Latitude and longitude of sites with repeated annual sampling from 2004-2007.

Appendix H: Number of sediment and *P. ceratophyllum* measurements sorted by sand, gravel, cobble, and boulder-bedrock categories for each site and year (2004-2007).

Appendix I: Correlation matrix of temperature, discharge, and nitrate variables. Temperature and nitrate correlation coefficients were derived from monthly averages. Discharge variables from USGS gage 02389150 were derived from January until the median *P. ceratophyllum* sample date. Statistical significance at p = 0.05 and at p = 0.06-0.09 is indicated by double and single asterix, respectively.

Appendix J: Comparison of site attributes and *Podostemum ceratophyllum* biomass measurements among studies of bedrock outcrops. Months of highest and lowest biomass are presented, or are presented as N/A if they could not be determined from the study.

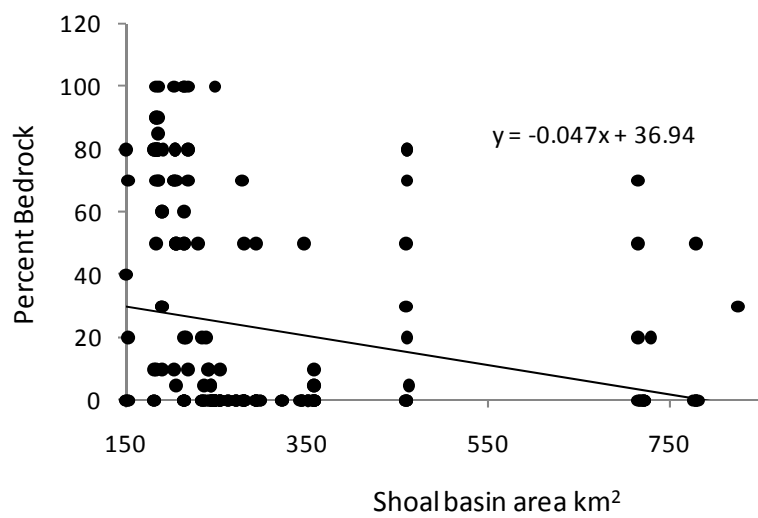
Appendix A.

Waypoint	Site ID	Latitude (N)	Longitude (W)	Width of flood-prone area (m)	Slope	Mannings n	Cross-sectional area (m ²)	Width (m)	Maximum depth (m)	Bank height (m)	Mean depth (m)
28	4800	34.299314	-84.272543	197	0.48	0.029	126	82	2.2	3.4	1.5
113	4200	34.334396	-84.245235	42	0.34	0.023	66	33	2.7	5.1	2.0
117	4300	34.322326	-84.23337	45	0.22	0.024	75	37	2.6	5.2	2.0
139	139	34.395455	-84.042559	34	0.33	0.024	41	30	1.9	3.8	1.3
143	143	34.39456	-84.045015	153	1.38	0.025	41	28	1.9	3.4	1.4
147	147	34.390253	-84.044496	120	0.77	0.033	43	23	2.2	3.5	1.9
149	149	34.388646	-84.043957	18	0.59	0.031	24	18	1.6	2.9	1.3
255	3000	34.355874	-84.135718	22	0.42	0.029	29	21	1.6	3.8	1.4
258	3115	34.356369	-84.1441	222	1.26	0.027	50	36	2.4	3.6	1.4
268	3305	34.368742	-84.154811	103	0.71	0.029	51	25	2.4	3.7	2.0
272	3315	34.372382	-84.161124	34	0.49	0.029	47	26	2.1	4.1	1.8
288	3605	34.367223	-84.198455	13	0.36	0.025	71	42	2.0	4.7	1.7
298	3905	34.355584	-84.213557	96	0.92	0.028	88	33	3.2	5.1	2.7
299	3800	34.336261	-84.245748	45	0.34	0.027	56	40	2.3	4.8	1.4
393	4715	34.303072	-84.244419	152	0.44	0.020	71	61	2.5	5.3	1.2

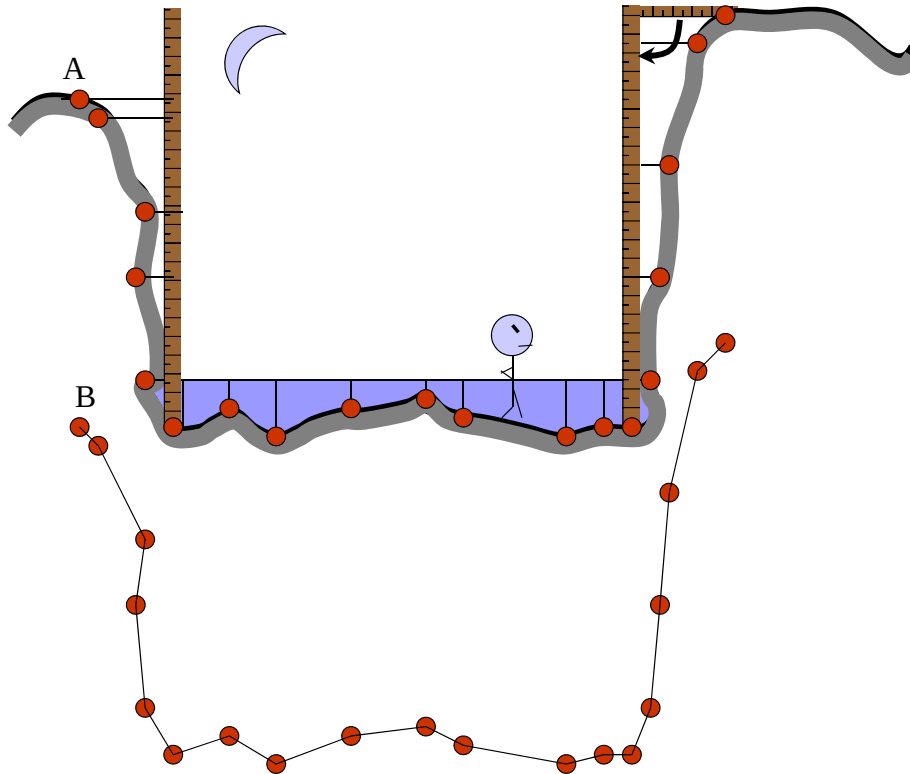
Waypoint	<i>Podostemum ceratophyllum</i> occurrence	<i>P. ceratophyllum</i> average maximum length (mm)	D16 (mm)	D35 (mm)	D50 (mm)	D65 (mm)	D84 (mm)	D95 (mm)	Proportion fines	Proportion gravel	Proportion cobble	Proportion boulder	Proportion bedrock
28	0.341	247	0	8	24	67	188	330	0.31	0.30	0.23	0.10	0.06
113	0.036	76	0	0	8	21	38	58	0.46	0.50	0.04	0.00	0.00
117	0.058	62	0	5	10	17	26	62	0.27	0.68	0.05	0.00	0.00
139	0.158	66	0	3	12	17	32	53	0.33	0.64	0.03	0.00	0.00
143	0.115	101	0	6	18	27	48	127	0.34	0.55	0.11	0.00	0.00
147	0.291	112	1	42	68	89	140	229	0.16	0.28	0.47	0.03	0.05
149	0.156	73	1	26	49	71	131	250	0.17	0.40	0.32	0.05	0.06
255	0.180	50	1	18	31	48	94	156	0.16	0.57	0.23	0.02	0.03
258	0.185	96	0	12	21	36	56	88	0.29	0.61	0.10	0.00	0.00
268	0.269	119	1	15	26	35	62	91	0.21	0.60	0.14	0.00	0.05
272	0.214	93	1	23	35	49	81	155	0.23	0.53	0.21	0.02	0.00
288	0.230	105	0	9	16	26	62	135	0.28	0.54	0.12	0.03	0.03
298	0.148	83	5	22	30	48	96	209	0.12	0.58	0.21	0.04	0.05
299	0.314	110	0	11	26	37	58	106	0.23	0.64	0.11	0.00	0.02
393	0.030	4	0	2	4	9	39	85	0.32	0.58	0.10	0.00	0.00

Waypoint	Wetted perimeter (m)	Hydraulic radius (m)	Width to depth ratio	Shoal length (m)	Entrenchment ratio	Shear stress (kg/m ²)	Shear velocity (cm/sec)	Unit stream power (kg/m/sec)	Froude number	Threshold sediment size (mm)
28	84.5	1.5	53	58	2.4	35.1	8.1	23.3	0.7	154
113	36.4	1.8	16	30	1.3	30.3	7.5	26.7	0.8	115
117	38.5	1.9	18	57	1.2	21.2	6.3	14.2	0.5	58
139	32.2	1.3	22	27	1.1	20.4	6.2	12.5	0.6	53
143	31.1	1.3	20	30	5.4	88.0	12.8	110.5	2.2	923
147	27.5	1.6	12	68	5.3	58.9	10.5	52.0	0.7	422
149	20.2	1.2	14	39	1.0	33.8	7.9	21.2	0.6	142
255	25.2	1.2	16	73	1.0	23.5	6.6	13.9	0.4	70
258	40.1	1.3	26	40	6.1	77.7	12.0	85.6	1.7	724
268	27.8	1.8	12	53	4.1	64.3	10.9	65.1	1.0	500
272	29.0	1.6	15	131	1.3	39.1	8.5	29.8	0.7	190
288	45.2	1.6	25	91	0.3	28.0	7.2	19.9	0.6	99
298	43.1	2.0	13	52	2.9	92.0	13.1	133.3	1.1	1007
299	45.7	1.2	29	59	1.1	20.6	6.2	11.9	0.5	54
393	63.2	1.1	52	63	2.5	24.4	6.7	18.9	1.1	76

Appendix B.



Appendix C.



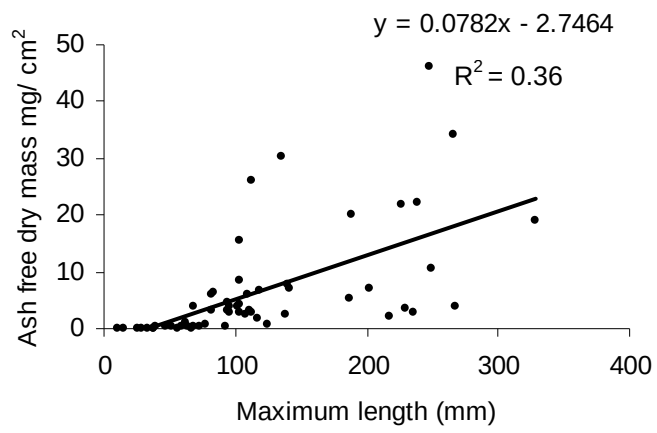
Steps- channel banks

1. Prop stadia vertically against channel bank.
2. Stand 6-9 m from stadia within clear line of sight of stadia and bank.
3. With arm fully extended, hold pencil horizontally such that the stadia appears to the left of the pencil.
4. The y-coordinate is the location on the stadia where the pencil intersects the stadia.
5. Hold the pencil where it appears to intersect the channel bank (red dots on bank).
6. With arm fully extended, rotate pencil (black arrow) to a vertical position while keeping the stadia visually to the left of the pencil.
7. Using the demarcations on the stadia, estimate the length of the pencil and use that value as the x-coordinate.
8. Repeat for other bank.

Steps- channel bed

1. With stadia standing against the bank, the base of the stadia (SB) is $x, y = 0, 0$.
2. Measure the water depth at the stadia.
3. At 10 ft intervals or at major changes in bed topography, measure water depth (WD).
4. Subtract the WD from the stadia depth to determine elevation relative to SB.
5. Add distance from depth measurement to SB x-coordinate to determine x-coordinate at the depth measurement.

Appendix D.



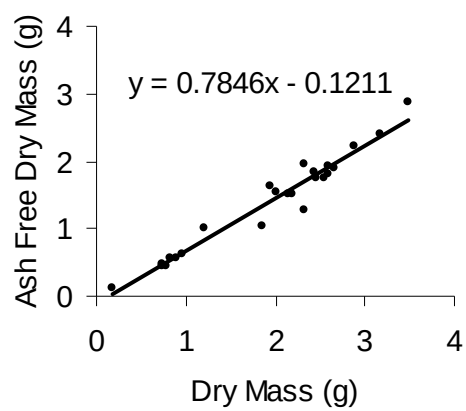
Appendix E.

	h	amp	plc	pc	pss	pcu	blg	unu	spg	pCgs	largely unmapped	Enters river from North (N), South (S), East (E), West (W), etc.	Alluvial shoal <200 m downstream from confluence
Creek													
Palmer	x	x	x	x		x	x					N	Yes
Russell	x	x	x	x		x	x					N	Yes
Shoal			x	x						x	x	N	Yes
Amicalola										x	x	N	Yes
Tobacco Pouch Branch											x	NW	Yes
Hurricane											x	W	Yes
Settingdown								x				ESE	No
Black Mill									x		x	S	No
Brewton									x		x	S	No
Camp			x	x	x							NE	No
Yellow										x	x	N	No

Appendix E. (*continued*)

Canton Formation		
	h	Helen member: metagraywacke and biotite-garnet-muscovite-biotite-quartz schist +/- staurolite with minor amphibolite (amp) that locally contains interlayered chlorite schist.
	plc	Palmer Creek member: thinly layered biotite-quartz schist +/- garnet and /or hornblende with garnet-biotite-muscovite-quartz schist and minor amphibolite (amp).
	pc	Proctor Creek Member: silvery muscovite-garnet-biotite-quartz schist.
	pss	pyrite-sericite-quartz schist +/- chlorite and/or hornblende with minor amphibolite (amp).
Univeter Formation		
	unu	Univeter undifferentiated: massive to thinly layered amphibolite interlayered with minor biotite-hornblende-plagioclase-quartz gneiss and micaceous iron formation.
Pumpkinvine Creek Formation		
	pcu	Pumpkinvine Creek undifferentiated: thinly layered to massive amphibolite/amphibole gneiss, lesser amounts of very coarsely porphyroblastic garnet-biotite-hornblende-quartz-plagioclase gneiss +/- calcite and/or staurolite, and iron formation.
	blg	Barlow gneiss Member: muscovite-biotite-plagioclase-quartz gneiss (metatuff?) containing flattened porphyroblasts of blue quartz and /or plagioclase. Locally interlayered with amphibolite.
Lithologies northwest and southeast of study area		
	spg	Sandy Springs Group: biotite gneiss, muscovite-biotite schist, amphibolite, micaceous quartzite, and kyanite-staurolite schist. Migmatization is widespread.
	pCgs	Great Smokey Group: metagraywacke, locally conglomeratic metasandstone, muscovite-biotite-quartz schist, and minor amphibolite.

Appendix F.



Appendix G.

Waypoint	Alternate Waypoint	Latitude (N)	Longitude (W)
113		34.334396	-84.245235
117		34.322326	-84.233370
255		34.355874	-84.135718
258		34.356369	-84.144100
268		34.368742	-84.154811
272		34.372382	-84.161124
280		34.361739	-84.186666
288		34.367223	-84.198455
298		34.355584	-84.213557
139	474	34.395455	-84.042559
147	479	34.390253	-84.044496

Appendix H.

2004

Site	Data	Boulder and bedrock	Cobble	Gravel	Sand	Grand Total
WP113	# of sediments with <i>P. ceratophyllum</i>		0	4	0	4
	# of sediments measured		1	58	52	111
WP117	# of sediments with <i>P. ceratophyllum</i>		3	9	0	12
	# of sediments measured		3	140	64	207
WP255	# of sediments with <i>P. ceratophyllum</i>	0	4	18	0	22
	# of sediments measured	6	18	78	20	122
WP258	# of sediments with <i>P. ceratophyllum</i>		2	18	0	20
	# of sediments measured		5	69	31	105
WP268	# of sediments with <i>P. ceratophyllum</i>	4	2	22	0	28
	# of sediments measured	5	5	73	12	95
WP272	# of sediments with <i>P. ceratophyllum</i>	0	14	35	0	49
	# of sediments measured	5	25	176	56	262
WP280	# of sediments with <i>P. ceratophyllum</i>	45	4	6	0	55
	# of sediments measured	80	6	40	20	146
WP288	# of sediments with <i>P. ceratophyllum</i>	4	7	15	0	26
	# of sediments measured	5	11	66	64	146
WP298	# of sediments with <i>P. ceratophyllum</i>	2	6	8	0	16
	# of sediments measured	7	16	70	15	108
WP139/474	# of sediments with <i>P. ceratophyllum</i>		0	26	0	26
	# of sediments measured		1	103	61	165
WP147/479	# of sediments with <i>P. ceratophyllum</i>	6	22	20	0	48
	# of sediments measured	13	50	76	28	167
Total # of sediments with <i>P. ceratophyllum</i>		61	64	181	0	306
Total # of sediments measured		121	141	949	423	1634

2005

Site	Data	Boulder and bedrock	Cobble	Gravel	Sand	Grand Total
WP113	# of sediments with <i>P. ceratophyllum</i>		0	1	0	1
	# of sediments measured		1	65	43	109
WP117	# of sediments with <i>P. ceratophyllum</i>		0	4	0	4
	# of sediments measured		1	89	57	147
WP255	# of sediments with <i>P. ceratophyllum</i>	0	4	8	0	12
	# of sediments measured	1	9	83	26	119
WP258	# of sediments with <i>P. ceratophyllum</i>	1	1	17	0	19
	# of sediments measured	1	5	62	34	102
WP268	# of sediments with <i>P. ceratophyllum</i>	10	3	4	0	17
	# of sediments measured	14	3	59	25	101
WP272	# of sediments with <i>P. ceratophyllum</i>	1	6	19	0	26
	# of sediments measured	2	15	106	47	170
WP280	# of sediments with <i>P. ceratophyllum</i>	51	1	3	0	55
	# of sediments measured	76	5	19	32	132
WP288	# of sediments with <i>P. ceratophyllum</i>	2	5	15	0	22
	# of sediments measured	5	12	84	37	138
WP298	# of sediments with <i>P. ceratophyllum</i>	2	5	3	0	10
	# of sediments measured	11	16	71	21	119
WP139/474	# of sediments with <i>P. ceratophyllum</i>		1	5	0	6
	# of sediments measured		1	80	26	107
WP147/479	# of sediments with <i>P. ceratophyllum</i>	1	16	8	0	25
	# of sediments measured	3	30	46	23	102
Total # of sediments with <i>P. ceratophyllum</i>		68	42	87	0	197
Total # of sediments measured		113	98	764	371	1346

Appendix H (continued)

2006

Site	Data	Boulder and bedrock	Cobble	Gravel	Sand	Grand Total
WP113	# of sediments with <i>P. ceratophyllum</i>			6	0	6
	# of sediments measured			76	54	130
WP117	# of sediments with <i>P. ceratophyllum</i>		3	6	0	9
	# of sediments measured		5	86	34	125
WP255	# of sediments with <i>P. ceratophyllum</i>	1	3	20	0	24
	# of sediments measured	5	12	104	27	148
WP258	# of sediments with <i>P. ceratophyllum</i>	1	4	31	0	36
	# of sediments measured	4	5	89	26	124
WP268	# of sediments with <i>P. ceratophyllum</i>	2	3	18	0	23
	# of sediments measured	7	8	70	46	131
WP272	# of sediments with <i>P. ceratophyllum</i>		4	24	0	28
	# of sediments measured		6	76	33	115
WP280	# of sediments with <i>P. ceratophyllum</i>	61	1	7	0	69
	# of sediments measured	82	3	18	26	129
WP288	# of sediments with <i>P. ceratophyllum</i>	4	7	23	1	35
	# of sediments measured	4	11	55	35	105
WP298	# of sediments with <i>P. ceratophyllum</i>	5	6	8	0	19
	# of sediments measured	12	16	79	18	125
WP139/474	# of sediments with <i>P. ceratophyllum</i>			5	0	5
	# of sediments measured			77	41	118
WP147/479	# of sediments with <i>P. ceratophyllum</i>	1	19	17	0	37
	# of sediments measured	1	29	71	12	113
Total # of sediments with <i>P. ceratophyllum</i>		75	50	165	1	291
Total # of sediments measured		115	95	801	352	1363

2007

Site	Data	Boulder and bedrock	Cobble	Gravel	Sand	Grand Total
WP113	# of sediments with <i>P. ceratophyllum</i>		0	9	0	9
	# of sediments measured		1	46	60	107
WP117	# of sediments with <i>P. ceratophyllum</i>		1	10	0	11
	# of sediments measured		1	73	28	102
WP255	# of sediments with <i>P. ceratophyllum</i>	0	3	22	0	25
	# of sediments measured	1	8	68	23	100
WP258	# of sediments with <i>P. ceratophyllum</i>		1	19	0	20
	# of sediments measured		4	77	42	123
WP268	# of sediments with <i>P. ceratophyllum</i>	2	7	26	0	35
	# of sediments measured	5	9	61	25	100
WP272	# of sediments with <i>P. ceratophyllum</i>		4	24	0	28
	# of sediments measured		14	76	31	121
WP280	# of sediments with <i>P. ceratophyllum</i>	63	1	5	0	69
	# of sediments measured	76	3	16	15	110
WP288	# of sediments with <i>P. ceratophyllum</i>	4	6	43	0	53
	# of sediments measured	4	10	94	17	125
WP298	# of sediments with <i>P. ceratophyllum</i>	6	5	8	0	19
	# of sediments measured	9	20	56	15	100
WP139/474	# of sediments with <i>P. ceratophyllum</i>			6	0	6
	# of sediments measured			54	46	100
WP147/479	# of sediments with <i>P. ceratophyllum</i>	4	18	27	0	49
	# of sediments measured	6	27	58	11	102
Total # of sediments with <i>P. ceratophyllum</i>		79	46	199	0	324
Total # of sediments measured		101	97	679	313	1190

Appendix I.

		Temperature					Discharge					NO ₃ +NO ₂ -N				
		T-April	T-May	T-June	T-July	T-August	Minimum flow	Maximum flow	Average flow	Median flow	# Peak flow days	N-April	N-May	N-June	N-July	N-August
Temperature	T-April	1.00														
	T-May	0.13	1.00													
	T-June	-0.73	0.19	1.00												
	T-July	0.45	-0.17	0.14	1.00											
	T-August	-0.32	-0.18	0.77	0.70	1.00										
Discharge	Minimum flow	-0.07	-0.26	-0.62	-0.80	-0.85	1.00									
	Maximum flow	-0.64	0.65	0.79	-0.32	0.25	-0.30	1.00								
	Average flow	-0.26	0.07	-0.37	-0.97**	-0.83	0.92	0.09	1.00							
	Median flow	-0.18	0.05	-0.45	-0.94**	-0.87	0.94	0.01	1.00	1.00						
	# Peak flow days	-0.30	0.41	-0.17	-0.96**	-0.75	0.72	0.39	0.93	0.91	1.00					
NO ₃ +NO ₂ -N	N-April	0.59	0.32	-0.83	-0.46	-0.94**	0.64	-0.32	0.61	0.67	0.58	1.00				
	N-May	-0.46	0.78	0.43	-0.62	-0.20	0.05	0.89	0.45	0.39	0.73	0.13	1.00			
	N-June	0.19	0.14	-0.71	-0.78	-0.99**	0.90	-0.20	0.90	0.93*	0.81	0.89	0.25	1.00		
	N-July	0.95	-0.18	-0.98	-0.73	-0.93	1.00**	-0.60	0.88	0.91	0.61	0.91	-0.15	0.93	1.00	
	N-August	0.58	0.04	-0.94*	-0.44	-0.94**	0.76	-0.53	0.63	0.69	0.49	0.96	-0.10	0.90	0.99	1.00

Appendix J.

Study	River, State	Stream order	Basin area (km ²)	Physiographic province	Sample period	Lowest biomass (g AFDM/m ²)- month	Highest biomass (g AFDM/m ²)- month
This study	Etowah, GA	5th	459	Piedmont	Apr 2006 - Oct 2007	11 Sep	190 Sep
Grubaugh and Wallace 1995	Middle Oconee, GA	6th	1030	Piedmont	Aug 1991 - Jul 1992	297 Mar	1045 Nov
Nelson and Scott 1962	Middle Oconee, GA	6th	1030	Piedmont	Apr 1956 - Apr 1957	100 Jun	640 Jun
Hutchens et al. 2004	Little Tennessee, NC	7th	837-1129	Blue Ridge	Jul 1997 - Aug 1997	200 N/A	400 N/A
Grubaugh et al. 1997	Little Tennessee, NC	7th	837-1129	Blue Ridge	Jul 1991 - May 1992	122 N/A	212 N/A