

Multi-scale patterns of habitat use by Roanoke logperch (*Percina rex*) in
Virginia rivers: a comparison among populations and life stages.

Amanda Rosenberger

Dissertation submitted to the Faculty of Virginia Polytechnic Institute and State
University in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in

Fisheries and Wildlife Sciences

Paul Angermeier, Chairman

Eric Hallerman

Andrew Dolloff

Tammy Newcomb

Eric Smith

19 December 2002

Blacksburg, Virginia 24061-0321

Key Words: *Percina rex*, habitat use, model transferability, ontogeny, spatial scale,
endangered species

Copyright 2002, Amanda Rosenberger

Multi-scale patterns of habitat use by Roanoke logperch (*Percina rex*) in Virginia rivers: a comparison among populations and life stages.

Amanda Rosenberger

(ABSTRACT)

The Roanoke logperch (*Percina rex*) is a federally endangered large darter that occurs only within the Roanoke and Chowan drainages of Virginia. This dissertation examines multi-scale habitat use patterns by logperch in three river systems in Virginia, including comparisons among rivers and life stages.

The first study in this dissertation compares microhabitat use patterns of logperch among the Roanoke, Pigg, and Nottoway rivers. My objectives are to: 1) compare available microhabitat and microhabitat use by logperch among these rivers; and 2) examine the transfer of habitat models among rivers. Habitat availability in the three rivers indicates that the Nottoway River is least impacted by human activity, while the Pigg River is most impacted. The Roanoke and Pigg rivers are found within the same region of Virginia and share many habitat characteristics. Logperch consistently use silt free, loosely embedded gravel in all rivers and can occupy a variety of depths and velocities to accommodate substrate requirements. Microhabitat models transfer better between the similar Pigg and Roanoke rivers.

The second study in this dissertation compares micro- and meso-habitat use patterns by Roanoke logperch in the Roanoke and Nottoway rivers. My objectives are to: 1) compare micro- and meso-habitat use patterns of logperch in the Roanoke and Nottoway rivers; and 2) examine transfer of habitat models at both scales. An increase in scale from micro- to meso- habitat did not improve model transfer. Habitat selectivity and transfer was strongest at the microhabitat scale. Logperch appear to be microhabitat substrate specialists and mesohabitat generalists.

The final study in this dissertation examines ontogenetic patterns of habitat use by Roanoke logperch in the Roanoke and Nottoway rivers. My goals are to: 1) examine habitat use by three age classes of logperch and 2) compare ontogenetic patterns of

habitat use between the Roanoke and Nottoway rivers. In the Roanoke River, adult and subadult logperch primarily used run and riffle habitat, often over gravel substrate. Subadults were found in lower water velocities and more embedded microhabitats than adults. Young-of-year logperch were found in shallow, stagnant backwaters and secondary channels. In the Nottoway River, both adult and subadult logperch were found over sand and gravel in deep, low velocity pools and runs. Subadults were observed in slightly more silted, lower velocity habitat. Younger age classes of logperch appear to be more vulnerable to sedimentation caused by human activity.

Evidence in this dissertation strongly indicates that logperch have strict substrate requirements and the distribution of habitat types and pathways of dispersal will be critical for completion of the logperch life cycle. A watershed-level conservation approach that addresses sediment loading and preserves ecological processes that provide ephemeral, seasonal, and persistent types of habitat required over logperch ontogeny will be most effective for management geared towards the recovery of this endangered species.

Acknowledgments

First and foremost, I wish to thank Paul Angermeier, whose efforts, advice, and kindness made this work possible. Paul provided encouragement and logistical support that allowed me to reach my full potential. I also wish to thank my committee members, Eric Hallerman, Andy Dolloff, Tammy Newcomb, and Eric Smith. They always took time from their incredibly busy schedules to provide advice and commiseration. Eric Hallerman had a fresh perspective and encouraged my efforts to enlarge my graduate school experience outside of research. Andy Dolloff generated ideas and insight for data collection when I initiated this project. He also provided advice and information that helped me launch my career. Tammy Newcomb's expertise on instream flow studies and habitat modeling was invaluable. I appreciate her open-minded interest and advice concerning the methods I chose to use to complete this dissertation. Eric Smith provided himself and his students for invaluable statistical advice and was extremely patient with my lack of expertise.

The U.S. Fish and Wildlife Service and the Virginia Department of Game and Inland Fisheries provided funding for this project. Personnel from these agencies showed consistent interest and accompanied me on field excursions to learn more about the Roanoke logperch. I am particularly grateful to Mike Pinder, who arranged funding for this project and remained supportive and helpful throughout my tenure at Virginia Tech. I also wish to thank Virginia Tech, the Department of Fisheries and Wildlife Sciences, the American Fisheries Society, and the PEO sisterhood who provided additional funding through fellowships, scholarships, and awards.

A great many people helped with the extensive and intensive fieldwork required to complete this study. I apologize for any omissions. I wish to thank Till Rosenberger, Kevin Minga, Jason Dotson, Paul Vidonic, Mark Dugo, Kathy Finne, Eddie Leonard, Rob Woods, Greg Galbreath, Brett Albanese, Dan Nuckols, Jamie Roberts, Ginnie Lintecum, Powell Wheeler, Mike Pinder, Ryan Smith, and Paul Angermeier, who provided invaluable field help.

A great many people also helped me with earlier versions of this work, provided their ear and advice, and listened to presentations before they were worth hearing. Many

thanks to Till Rosenberger, Tim Copeland, Kirk Krueger, Pat Devers, Jamie Roberts, Don Orth, Brett Albanese, Kim Mattson, and the rest of the graduate student community at Virginia Tech for providing this help and their friendship which has made the last four and a half years at Virginia Tech worthwhile. I am particularly grateful to Penelope Pooler, with Statistics Consulting, who helped me slog through SAS and logistic regression.

Finally, like many graduate students, I must thank my family for their untiring and enthusiastic support. My parents and sister have listened with interest to constant fish chatter, and my parents continue to support me emotionally and financially as I move from location to location, sometimes as far as Africa, to pursue my passion. Till Rosenberger has been my greatest source of encouragement, my biggest fan, and constantly provides love, affection, inspiration, sanity, perspective, and child care. This work is dedicated to him and to my sweet and beautiful daughter, Nora Bailie Rosenberger.

Table of Contents

General Introduction	1
Chapter 1. Transferability of microhabitat associations of Roanoke logperch (<i>Percina rex</i>) among three rivers in Virginia	5
Introduction	5
Objectives.....	8
Methods.....	9
Study sites.....	9
Sampling methods	10
Data analysis.....	11
Results	13
Microhabitat availability.....	13
Univariate analysis of habitat use	14
Multivariate analysis of habitat use	16
Logistic regression analysis.....	17
Model transfer.....	17
Discussion	18
Habitat use patterns and habitat availability	18
Habitat model transfer	19
Conclusions	22
Chapter 2. Transferability of micro- and meso- habitat associations of Roanoke logperch (<i>Percina rex</i>) between the Roanoke and Nottoway rivers	40
Introduction	40
Objectives.....	42
Methods.....	44
Study sites.....	44
Mesohabitat sampling	44
Microhabitat sampling	46
Data analysis.....	47
Results	49
Habitat availability.....	49
Univariate analysis of micro- and meso-habitat use by Roanoke logperch	50
Multivariate analysis of micro- and meso-habitat use by Roanoke logperch	51
Logistic regression analysis.....	53
Model transfer.....	54
Discussion	54
Habitat availability and logperch habitat use in the Roanoke and Nottoway rivers	54
Habitat use patterns and life-history characteristics of Roanoke logperch	55
Model transferability and spatial scale of investigation.....	56
Implications	57
Chapter 3. Ontogenetic shifts in habitat use by the endangered Roanoke logperch (<i>Percina rex</i>)	73
Introduction	73
Objectives.....	75
Methods.....	76
Study sites.....	76
Fish survey methods	77
Habitat observations	77
Data analysis.....	78
Results	80
Habitat use descriptions	80
Univariate analysis.....	80
Multivariate analysis.....	82

Discussion	84
Ontogenetic shifts in habitat use	84
Differences between rivers in ontogenetic shifts	86
Conservation and management implications	87
General conclusions	103
Conservation of the Roanoke logperch	103
Broader implications	104
Literature Cited	106
Appendix A. Composite model of logperch habitat use	119
Appendix B. Observations of seasonal habitat use by Roanoke logperch	123
Vita	130

List of Tables

Table 1.1 Summary of microhabitat characteristics (mean \pm standard deviation) of pools, riffles, and runs in the Roanoke, Pigg, and Nottoway rivers. *Indicates a significant difference at the 0.05 level (ANOVA). Underlines indicate no significant difference between river pairs (Sheffe's multiple comparisons, $\alpha = 0.05$).....	24
Table 1.2 Canonical discriminant functions of a discriminant analysis comparing microhabitat availability among the Roanoke, Pigg, and Nottoway rivers (Figure 2)....	25
Table 1.3 A summary of habitat characteristics of locations where adult Roanoke logperch were observed during snorkeling surveys in the Roanoke, Pigg and Nottoway rivers.....	26
Table 1.4 Summary of PCA of logperch habitat use and habitat availability for the Roanoke, Pigg, and Nottoway rivers (see Figure 6) and loadings of seven habitat variables on the first two principal components and percent of total variance explained by each component.....	27
Table 1.5 Canonical discriminant functions for discriminant analysis of logperch habitat use for the Roanoke, Pigg, and Nottoway rivers (see Figure 7).....	28
Table 1.6 Summary of logistic regression models used to estimate probability of presence of Roanoke logperch in microhabitat locations in the Roanoke, Pigg, and Nottoway rivers, Virginia. Parameter estimates are maximum-likelihood estimates, and significance of each variable is based on Wald χ^2 . Significance of each model is based on a χ^2 of the -2 log-likelihood statistic	29
Table 1.7 The sensitivity and specificity of logistic regression models developed to predict the presence of Roanoke logperch in the Roanoke, Pigg, and Nottoway rivers.	

Underlined values indicate model verification. The remaining values indicate the transferability of models from one river to the next..... 30

Table 2.1 Summary of mesohabitat (A) and microhabitat (B) characteristics (mean ± standard deviation) of pools, riffles, and runs in the Roanoke and Nottoway rivers. *Indicates a significant difference between rivers at the 0.05 level (t-tests) 61

Table 2.2 Summary of mesohabitat characteristics of habitat units (pools, riffles, or runs) where adult Roanoke logperch were observed during snorkeling surveys in the Roanoke and Nottoway rivers, Virginia. *Indicates a significant difference at the 0.05 level (Mann-Whitney U tests)..... 62

Table 2.3 A summary of G-tests examining the frequency of logperch occurrences in meso- and micro-habitat categories relative to availability of those categories. A significant G-test indicates that logperch selected habitat categories disproportionately to their availability. The direction of this selection is presented for significant and marginally significant tests (NS = $P > 0.05$) 63

Table 2.4 A summary of microhabitat characteristics of point locations where adult Roanoke logperch were observed during snorkeling surveys in the Roanoke and Nottoway rivers, Virginia. *Indicates a significant difference at the 0.05 level (t-tests for continuous data, Mann-Whitney U tests for ranked data)..... 64

Table 2.5 Loadings of habitat variables on the first two principal components and percent of total variance accounted for by each component for (A) mesohabitat use and availability data and (B) microhabitat use and availability data in the Roanoke and Nottoway Rivers, Virginia 65

Table 2.6 Jack-knifed classification matrix (A) and canonical discriminant functions (B) of a discriminant analysis examining differences between mesohabitats containing logperch in the Roanoke and Nottoway rivers, Virginia..... 66

Table 2.7 Jack-knifed classification matrix (A) and canonical discriminant functions (B) of a discriminant analysis examining differences between the Roanoke and Nottoway rivers in logperch microhabitat use 67

Table 2.8 Summary of logistic regression models used to estimate probability of presence of Roanoke logperch in microhabitat and mesohabitat locations in the Roanoke and Nottoway rivers, Virginia. Parameter estimates are maximum-likelihood estimates, and significance of each variable is based on Wald chi-square. Significance of each model is based on a chi-square of the $-2 \log$ -likelihood statistic 68

Table 2.9 The sensitivity (ability to detect presence; “# of true presences” / [“# of true presences” + “# of false absences”]) and specificity (ability to detect absence; “# of true absences” / [“# of true absence” + “# of false presences”]) of logistic regression models developed to predict the presence of Roanoke logperch in the Roanoke and Nottoway rivers, Virginia, using mesohabitat (A) and microhabitat (B) use data. Underlined values indicate model verification. The remaining values indicate the transferability of models between rivers 69

Table 3.1 Habitat use by Roanoke logperch and available habitat in the Roanoke and Nottoway rivers, Virginia..... 89

Table 3.2 Comparison of habitat characteristics of pools, runs, and riffles in the Roanoke and Nottoway rivers, Virginia. * indicates significance at the 0.02 level for t- and Mann-Whitney U tests (Dunn-Sidak correction for multiple comparisons)..... 90

Table 3.3 Loadings of six habitat variables on the first two principal components and percent of total variance accounted for by each component for the Roanoke and Nottoway rivers, Virginia..... 91

Table 3.4 Canonical discriminant functions for two discriminant axes representing
multivariate habitat use of three age classes of Roanoke logperch..... 92

List of Figures

Figure 1.1 Map of the Roanoke, Pigg, and Nottoway rivers, Virginia, indicating sites selected for snorkeling surveys	31
Figure 1.2 Discriminant analysis of microhabitat availability measurements for the Roanoke, Pigg, and Nottoway rivers, Virginia. Axis labels are based on canonical discriminant functions of Factor 1 and 2. Circles represent 95% confidence intervals around the mean canonical value for each river.....	32
Figure 1.3 Proportional abundance of available habitat and proportional occurrence of adult logperch in habitat categories in the Roanoke (A), Pigg (B), and Nottoway (C) rivers, Virginia. Data were collected during summer sampling. * indicates a significant <i>G</i> -test at the 0.01 level (Dunn-Sidak correction for multiple tests). Significance indicates non-random selection	33
Figure 1.4 Mean habitat use (depth, mean velocity, and bottom velocity) of adult Roanoke logperch observed in the Roanoke, Pigg, and Nottoway Rivers, Virginia. *Indicates a significant difference at the 0.05 level (ANOVA, Scheffe’s multiple comparisons)	36
Figure 1.5 Mean use of substrate characteristics by adult Roanoke logperch observed in the Roanoke, Pigg, and Nottoway rivers, Virginia	37
Figure 1.6 A graphical presentation of principal component scores for microhabitat availability and use by Roanoke logperch in the Roanoke, Pigg, and Nottoway rivers, Virginia. The polygons circumscribe the area representing available microhabitat	38
Figure 1.7 Discriminant analysis of habitat use by Roanoke logperch in the Roanoke, Pigg, and Nottoway rivers. Ellipses around data points are 95% confidence intervals around mean canonical scores.....	39

Figure 2.1 Map of the Roanoke and Nottoway rivers, Virginia, indicating sites selected for snorkeling surveys for Roanoke logperch (*Percina rex*)..... 70

Figure 2.2 A graphic presentation of principal component scores for mesohabitats containing Roanoke logperch in the Roanoke and Nottoway rivers, Virginia. The polygon in each figure circumscribes the area representing available mesohabitats in each system, while the area curves next to the axes represent the relative frequency of mesohabitat availability locations 71

Figure 2.3 A graphic presentation of principal component scores for microhabitat locations where Roanoke logperch were observed in sites surveyed in the Roanoke and Nottoway rivers, Virginia. The polygon in each figure circumscribes the area representing available microhabitat in each system, while the area curves next to the axes represent the relative frequency of microhabitat availability locations 72

Figure 3.1 Map of the Roanoke and Nottoway rivers, Virginia, indicating sites selected for snorkeling surveys and areas surveyed for young-of-year Roanoke logperch (*Percina rex*) 93

Figure 3.2 Schematic of the “transect cross” technique used to quantify young-of-year habitat use..... 94

Figure 3.3 Proportional abundance of available habitat and proportional occurrence of observed adult, subadult and young-of-year logperch in habitat categories for the Roanoke River (A) and Nottoway River (B), Virginia. * indicates a significant *G* test at the 0.02 level (Dunn-Sidak correction for multiple tests). Significance indicates non-random selection of a habitat variable by the age class (A = adult, S = subadult, Y = young-of-year)..... 95

Figure 3.4 Mean habitat use of adult, subadult and young-of-year Roanoke logperch in the Roanoke River (A) and adult and subadult logperch in the Nottoway River (B), Virginia. Error bars indicate 95% confidence interval of the mean. * indicates a significant difference in habitat use (non-parametric multiple comparisons, $\alpha = 0.05$) 97

Figure 3.5 A graphic presentation of principal component scores for each age class of Roanoke logperch in the Roanoke River (A) and Nottoway River (B), Virginia. The polygon in each figure circumscribes the area representing available habitat in sampling sites, while the area curves on axes of the bottommost graph represent the relative frequency of availability locations 99

Figure 3.6 Discriminant analysis of habitat use by three age classes of Roanoke logperch in the Roanoke River, Virginia. Ellipses around data points are 95% confidence intervals around mean canonical scores 101

Figure 3.7 Discriminant analysis of habitat use of adult and subadult Roanoke logperch in the Nottoway River, Virginia. Ellipses around data points are 95% confidence intervals around mean canonical scores 102

General Introduction

Defined as a location or set of locations where an individual, population, or assemblage of fishes can find the chemical or physical characteristics required for completion of life history (Orth and White 1993), habitat quality has been linked to growth, survival, and reproduction parameters used in fish population dynamics studies (Breck et al. 1988, Hayes et al. 1996). Heterogeneity in environmental conditions that determine the distributional limit of a species can be viewed hierarchically, from regional to local scales (Tonn et al. 1990, Angermeier and Winston 1998, Angermeier et al. 2002). Large spatial patterns often reflect regional species pools and dispersal ability, while, within this regional distribution (e.g., drainage and/or physiography), numerous local environmental factors, including biotic and abiotic characteristics of the environment, directly influence the distribution of a species (e.g. Dunham et al. 2002). High endangerment and extinction rates among aquatic species (Master 1990, Williams et al. 1993, Etnier 1997) has led to many studies examining the habitat requirements of imperiled fishes and ecosystem-level processes that maintain suitable habitats (Schlosser and Angermeier 1995, Labbe and Fausch 2000). Such studies can provide valuable conservation tools, critical for reversing declines and restoring populations of imperiled species (Poff 1997). Habitat studies are valuable because habitat manipulation is one of the approaches that have been effective for managing threatened biota.

To use knowledge of habitat use by a species for conservation and management purposes, we must make certain assumptions: 1) observed habitat use reflects actual preferences of the study species; 2) observed habitat use is evolutionarily adaptive (i.e., enhances fitness); and 3) habitat use is characteristic of a species; therefore, habitat associations should be transferable among locations (Angermeier 1987, Baltz et al. 1987, Bozek and Rahel 1992). Controlled experiments can be used to examine the validity of these assumptions and determine mechanistic links between habitat use and life history requirements. However, if controlled experiments are infeasible due to logistic constraints or scarcity of the study species, comparative field studies can be instructive. In this dissertation, I have used a comparative approach to identify key habitat features for an endangered species endemic to Virginia, the Roanoke logperch (*Percina rex*). I

have completed three related field studies comparing this species' habitat use among populations, between two spatial scales, and among life history stages.

The Roanoke logperch (*Percina rex*) is a large darter that occurs only within the Roanoke and Chowan drainages of Virginia (Jenkins and Burkhead 1993). Within the Roanoke drainage, logperch can be found in the upper Roanoke, Pigg, and Smith rivers and some of their larger tributaries. Within the Chowan drainage, logperch are distributed along the fall zone between the piedmont and coastal plain physiographic provinces in the Nottoway River and its largest tributary, Stoney Creek. The greatest population densities of Roanoke logperch are in the upper Roanoke River (Burkhead 1983, Jenkins and Burkhead 1993) and in the Nottoway River drainage (Rosenberger and Angermeier 2002). Based on its limited distribution and the vulnerability of its largest population centers to urban and industrial stresses, Roanoke logperch have been placed on the federal endangered species list (Federal Register Vol. No. 159).

A comparison of habitat use among logperch populations can be used to identify habitat features that are consistently occupied across a variety of ecological conditions and population densities. These features are probably critical for determining the distributional limit of the species. The first study compares the microhabitat use patterns of logperch among three of its populations. My goals in this study are to: 1) describe and compare the characteristics of available microhabitat in the Roanoke, Pigg, and Nottoway rivers; 2) describe microhabitat preferences of Roanoke logperch in the three rivers; 3) compare use and preference of individual microhabitat parameters and multivariate habitat configurations among rivers; and 4) examine the transferability of habitat selectivity and habitat use patterns among rivers.

A comparison of habitat use over multiple scales can alter conclusions about the factors limiting a species, illustrate limitations in the data, and assist in avoiding errors of interpretation (Frost et al. 1988, Welsh and Perry 1998). The degree of an aquatic species' response to variation in environmental factors at multiple scales can identify what scales are most relevant for the target species and most appropriate for management actions (Bult et al. 1998). The second study identifies occupied habitat features at meso- and micro- scales for two populations of the Roanoke logperch. My goals in this study are: 1) to describe differences between the Roanoke and Nottoway rivers in available

micro- and meso- habitat; 2) compare habitat use patterns of Roanoke logperch in both rivers at micro- and meso- habitat scales; and 3) examine whether an increase in scale of observation from micro- to meso- habitat improves the transferability of habitat models.

Finally, understanding of habitat requirements over a species' life history gives insight into distributional limiting factors over all life stages and reveals generalities about the species' habitat requirements. Knowledge of a species' habitat use over ontogeny support management actions preserving ecological processes that create the variety of habitat patches required over life history. The last study documents and quantifies shifts in habitat use by Roanoke logperch over ontogeny in two of its populations. I examine the habitat use of individual Roanoke logperch in three size categories in the Roanoke River and two size categories in the Nottoway River to determine whether: 1) age classes of logperch exhibit habitat selectivity, 2) age classes differ in habitat use, and 3) ontogenetic patterns of habitat use differ between the Roanoke and Nottoway populations.

Results from these three studies collectively indicate factors limiting the distribution of Roanoke logperch in the Roanoke, Pigg, and Nottoway rivers and indicate broader ecological patterns for this species. Relating differences in habitat use among populations, scales, and life stages provides insight to mechanisms explaining logperch habitat use, what scale we can most effectively manage logperch habitat, and factors causing shifts in habitat use over Roanoke logperch ontogeny. In all chapters, I discuss conservation and management implications of these comparative studies and suggest strategies that will preserve habitat mosaics required over Roanoke logperch life history.

Some general aspects of life history, habitat use, and behavior of Roanoke logperch are summarized in previous research (Jenkins 1977, Burkhead 1983, Jenkins and Burkhead 1993, Ensign 1995); however, most of this information is based in the upper Roanoke River during warm months. Adult logperch in the Roanoke River are typically found in deep, high velocity riffle and run habitats, while young and juveniles have been observed in slow runs and pools, where they are frequently observed over clean sand bottoms. Spawning of logperch typically occurs in scoured, deep riffles and runs (Burkhead 1983). The eggs are adhesive and demersal, and larvae are thought to drift to calm water areas after hatching (Burkhead 1983). Because standard

electrofishing techniques collect very small logperch inefficiently, Burkhead (1983) only observed two young-of-year (YOY) over the duration of his two-year study. Both were observed in shallow, sandy pool margins. Roanoke logperch of all age classes seem intolerant of moderately to heavily silted substrates in the Roanoke River, possibly due to their feeding behavior unique to the subgenus *Percina*. Logperch use their conical snout to flip gravel and feed on exposed invertebrates. This exploits prey sheltered beneath rocks that may be unavailable to other benthic fishes; however, this feeding behavior relies on the availability of loosely embedded substrate.

Major gaps in our knowledge of Roanoke logperch habitat use and life history include seasonal and ontogenetic habitat use, movement by individual fishes, and differences in age structure and demographics among populations. Further, outside of the Roanoke River, habitat use by other populations of logperch is largely unknown. Differences in habitat availability between these rivers may influence patterns of habitat use. This basic information will be critical to making recovery efforts effective and will enhance managers' understanding of factors that limit logperch distribution and abundance relevant to the long-term viability of logperch populations.

Chapter 1. Transferability of microhabitat associations of Roanoke logperch (*Percina rex*) among three rivers in Virginia

INTRODUCTION

Among the most important goals of ecology is the identification of factors that limit the distributions of species. These factors can be viewed hierarchically, from regional to local scales (Tonn et al. 1990, Angermeier and Winston 1998). Heterogeneity in environmental conditions, in part, regulates heterogeneity in species distributions (Angermeier et al. 2002). Large spatial patterns of species distribution often reflect regional species pools and dispersal ability, while within a particular region (e.g., a drainage or physiography), numerous local biotic and abiotic characteristics of the environment determine the distributional limit of a species (e.g., Dunham et al. 2002). Defined as a location or set of locations where fish can find the chemical and physical characteristics required for life history (Orth and White 1993), fish habitat strongly influences distribution via effects on growth, survival, and reproductive success (Breck et al. 1988, Hayes et al. 1996).

The ability to predict distributions of fish and understand the factors that limit persistence in certain habitats is important for informed management and conservation of imperiled species. Habitat models can help assess habitat suitability, estimate habitat loss due to natural or anthropogenic disturbance, and predict fish distributions (Orth and Maughan 1982, Moyle and Baltz 1985, McClendon and Rabeni 1987, Orth 1987). Additionally, models can indicate which habitat configurations are most limiting for a species at selected scales. As our understanding of habitat associations advances, so does the effectiveness and scientific bases of management decisions. For example, the health of a population most limited by the availability of woody debris could be enhanced by the addition of wood to stream reaches and riparian restoration throughout the watershed. Models that predict the presence or absence of a species within reaches and watersheds are typically of most interest to managers because manipulations at these scales, such as stream bank stabilization or stream corridor restoration, are generally the most logistically and socially feasible.

The use of habitat models for management purposes implies certain assumptions: 1) observed habitat use reflects fish preferences; 2) observed habitat use is evolutionarily adaptive (i.e., enhances fitness); and 3) habitat use is characteristic of a species; therefore, some habitat associations should be transferable among locations (Angermeier 1987, Baltz et al. 1987, Bozek and Rahel 1992). If controlled experiments are not feasible to examine the validity of these assumptions due to logistic constraints or scarcity of the study species, comparative field studies can be instructive. Understanding of similar distributional patterns and consistently used habitat configurations across a range of local conditions can lend insight regarding factors limiting the distribution of species. Further, results of such studies can indicate which habitat use patterns are and are not transferable between populations, leading to simpler, broadly applicable models.

Transferable habitat models are particularly useful for conservation purposes because they can identify potential habitat in areas that are poorly surveyed, identify areas for reintroduction, justify protection of areas that are not occupied, and indicate factors limiting distribution (Angermeier et al. 2002). Further, a single, transferable habitat model obviates the need for costly, time-consuming site-specific habitat models and is likely to indicate broad ecological patterns of a species. Unfortunately, the predictive power of many habitat models has been limited to the locality in which they were originally developed, and model transfers have met with mixed success (Bowlby and Roff 1986, Angermeier 1987, Layher et al. 1987, Hubert and Rahel 1989, Rabeni and Sowa 1996, Leftwich et al. 1997, Dunham et al. 2002).

Most habitat models focus on microhabitat use by species rather than other scales of resolution (e.g. Freeman et al. 1997). In such cases, biologists assume that abundance of the target species is primarily controlled by local environmental factors that determine available microhabitat. This is often an erroneous assumption; research has demonstrated that large-scale processes can determine the overall health of a population by creating, maintaining, and destroying suitable habitat patches required by species over their life history (Schlosser and Angermeier 1995, Labbe and Fausch 2000). Microhabitat studies, however, can lend insight to population-level processes, and are most instructive when coupled with studies at larger scales. Microhabitat remains the most feasible and most commonly-used scale for habitat studies and is, therefore, the focus of this study.

A model developed in one system is unlikely to precisely predict microhabitat use in another because of obvious and subtle selective differences among systems in local conditions. However, areas within the same region that share similar assemblages, habitat availability, and other constraints may show considerable overlap in species microhabitat use because these areas are more likely to share factors that limit the distribution of the target species (Belaud et al. 1989, Tonn et al. 1990). Other strategies that can improve the transferability of microhabitat models include the use of composite models from two or more sites, regions, or age classes that incorporate a variety of limiting factors (Bozek and Rahel 1992, Goshens and Orth 1994). Further, models that incorporate a habitat feature that can be mechanistically linked to the life history requirements of the species are more likely to transfer effectively (Bateman and Li 2001).

It is particularly challenging to create a transferable, broadly applicable habitat model for imperiled species characterized by low numbers or variable population sizes. At low population densities, the probability of detecting an individual within a certain habitat configuration is low, weakening models that characterize habitat preference by contrasting occupied and unoccupied habitat configurations. Populations with highly variable densities may show density-dependent patterns of habitat use in response to spatial variation in biotic interactions and differential use of less-preferred habitat configurations (Angermeier et al. 2002). Despite these challenges, the creation of broadly applicable models for the management of imperiled species is critical because such models are most likely to incorporate relevant ecological factors.

This study addresses the transferability of microhabitat associations of a federally endangered darter species endemic to Virginia, *Percina rex* (Federal Register Vol. 159). The Roanoke logperch is a large darter that occurs in four distinct populations within the Roanoke and Chowan drainages of Virginia (Jenkins and Burkhead 1993, Figure 1.1). The distributional pattern of this species offers a unique opportunity to examine regional patterns of microhabitat use. Existing knowledge of Roanoke logperch habitat use was described in Burkhead (1983) and Jenkins and Burkhead (1993) and is based exclusively on data collected in the Roanoke River. Adult logperch in this river are typically found in deep, high velocity riffle and run habitats in clear, medium size, and medium gradient rivers. Roanoke logperch seem intolerant of moderately to heavily silted substrates, possibly due to their feeding

behavior unique to the subgenus *Percina*. Logperch use their conical snout to flip gravel and feed on exposed invertebrates (Burkhead 1983, Jenkins and Burkhead 1993). This exploits prey sheltered beneath rocks that may be unavailable to other benthic fishes; however, this feeding behavior relies on the availability of loosely embedded substrate. Habitat use by logperch outside of the Roanoke River, including populations in the Pigg and Nottoway rivers, was largely unknown.

OBJECTIVES

My goals in this study are to: 1) describe and compare the characteristics of available microhabitat in the Roanoke, Pigg, and Nottoway rivers; 2) describe microhabitat preferences of Roanoke logperch in the three rivers; 3) compare use and preference of individual microhabitat parameters and multivariate habitat configurations among rivers; and 4) examine the transferability of habitat selectivity and habitat use patterns among rivers. Results will indicate which factors are limiting the distribution of Roanoke logperch in the Roanoke, Pigg, and Nottoway rivers and indicate broader ecological patterns of this species. Relating differences in habitat use among populations to differences in habitat availability will provide insight into mechanisms determining logperch habitat use. I also use these results to examine if habitat models and patterns for Roanoke logperch transfer more successfully between rivers that share regional characteristics and species pools (the Pigg and Roanoke rivers). Further, I examine which statistical methods are most useful in predicting suitable habitat among rivers.

Using univariate techniques, I examine differences among rivers in selection and use of individual habitat parameters. However, because logperch are likely responding to multiple habitat variables, multivariate techniques are also used. Principal components analysis (PCA) is used primarily as an exploratory method to examine overall availability and selection of habitat configurations as well as differences among rivers in habitat availability and use. I also use canonical discriminant analysis to quantitatively examine multivariate differences among systems in habitat use and availability. For these analyses, all habitat variables are considered. Because discriminant analysis emphasizes differences among pre-determined groups and identifies variables that differ the most among groups, it is

used to identify which variables account for significant differences among rivers in both available and used habitat configurations. I use three separate logistic regression models to examine habitat use patterns of logperch for each river. These models use only the subset of habitat variables found important for predicting the presence and absence of logperch in the river in which the model was developed. These models were transferred to each river system and assessed based on the proportion of correct predictions.

METHODS

Study Sites

Within the Roanoke drainage, isolated populations of logperch occur in the upper Roanoke, Pigg, and Smith rivers. Within the Chowan drainage, logperch are distributed along the fall zone between the piedmont and coastal plain physiographic provinces in the Nottoway River. The greatest population densities of Roanoke logperch are in the upper Roanoke River (Burkhead 1983, Jenkins and Burkhead 1993) and in the Nottoway River drainage (Rosenberger and Angermeier 2002). In this study, I concentrated on the populations in the Roanoke, Pigg, and Nottoway rivers (Figure 1.1). The Roanoke and Pigg rivers are located in western Virginia and have similar assemblages and regional conditions. The Roanoke River is a clear, coolwater, high gradient system, and the Pigg River in the Roanoke River drainage is a coolwater, medium gradient system. Cattle farming and construction along the stream banks contribute heavy silt loads to these rivers. The Nottoway River is located in eastern Virginia in the Chowan drainage. This river is tannin-stained, warmwater, and lowland (Jenkins and Burkhead 1993). The Nottoway River is similar in gradient to the Roanoke and Pigg rivers only in the Fall Zone between the Piedmont and Coastal Plain physiographic provinces, where riffle and run habitat occur. The Nottoway River fauna is closely related to the fauna of the Roanoke River due to historic connection between the Roanoke and Chowan rivers; however, the Nottoway River contains additional species characteristic of the Coastal Plain and lower Piedmont. The Nottoway River has an intact riparian zone that contributes woody debris and prevents heavy sedimentation from human activity in its watershed.

Stratified, systematic sampling of habitat increases the probability of detecting discontinuities in a species' distribution (Angermeier et al. 2002); therefore, I systematically sampled sites that contained a riffle, run, and pool, the most commonly studied strata in stream reaches. I considered high gradient areas with convex stream bottoms, turbulent water surfaces, and fast water to be riffle habitat. Pools were deep, low gradient, slow moving areas with concave stream bottoms (following Beschta and Platts 1986). Runs were defined as intermediate gradient areas with flat stream bottoms, fast water, and smooth water surfaces (Vadas and Orth 1998). In the summer of 1999, a reachwide inventory of 10 km of the Roanoke River and 20 km of the Nottoway River was conducted using the basinwide visual estimation technique described in Dolloff et al. (1993). These lengths allowed the sampling of a wide range of habitat types. For each river, every tenth riffle-run-pool site along the reachwide inventory was selected for summer quantitative underwater observation using line transect snorkeling methods (eight sites per river; Roanoke River site lengths: 75-141m; Nottoway River site lengths: 79-150m; Figure 1.1). Six riffle-run-pool sites were selected from the Pigg River downstream from the town of Rocky Mount based on river accessibility (site lengths: 74-121m; Figure 1.1).

Sampling methods

Summer survey observations for each site were made via the line-transect snorkeling methods described in Ensign et al. (1995). One to three parallel lines oriented with river flow were marked with yellow line on the day of sampling. Spacing between lines was a minimum of 1.5 times maximum underwater visibility on the day of sampling. The length of the lines was based on the length of the habitat units but did not exceed 50m per unit (150m per site). Visibility was determined by suspending a Secchi disk in the water column in front of a snorkeler. The snorkeler moved away from the disk until the black patterns on the disk were no longer distinguishable from the water. The distance between the snorkeler and the disk was measured and served as the maximum visibility for that day. Surveys were not conducted if maximum visibility was less than 1.5 meters (Leftwich et al. 1997).

To minimize effects of disturbance and to allow fish to settle, snorkelers did not begin sampling until at least one hour after placement of the transect lines. Snorkelers entered the water downstream of the area to be sampled and moved slowly upstream along the lines,

keeping the center of the body over the line. Each observer scanned the stream bottom, mid-water, and upper-water column directly in front and to both sides of the line of travel. When a Roanoke logperch was sighted, a numbered weighted marker was placed on the stream bottom precisely where the fish was first spotted. The number-code of markers and age class (adult or subadult) were recorded on dive slates. This study focuses on adult logperch only. Double counting of logperch was avoided by simultaneously sampling all three transect lines with snorkelers staying even with each other while moving upstream. Continuous communication between snorkelers also minimized double counting. After the riffle-run-pool sequence was sampled, snorkelers returned to the base of transects to count markers and collect habitat data.

Microhabitat data included water depth, bottom and mean water velocities, and point substrate size (9-category Wentworth scale). I also recorded substrate characteristics within a 1-m² area around the marker, including dominant and subdominant substrate size, embeddedness (5 categories: 1 = ≥ 95% embedded, 2 = 50-94%, 3 = 25-49%, 4 = 5-24%, 5 = 0-5%, i.e. exposed), and silt cover (5 categories: 1 = 76-100% of area blanketed with deposited silt, 2 = 51-75%, 3 = 26-50%, 4 = 1-25%, 5 = 0%). To record microhabitat availability, I placed horizontal transects along the wetted width of the river at 10-meter intervals along the length of the site within 24 hours of the snorkeling run. Every three meters along the horizontal transects, depth, mean and bottom water velocities, silt cover were recorded. I also recorded dominant and subdominant substrates, silt cover, and embeddedness within a 1-m² area.

Data Analysis

All data analyses, with the exception of the logistic regression models, were performed using SYSTAT (Version 9, Copyright © SPSS Inc., 1998). I used analysis of variance (ANOVA) to compare microhabitat availability among the Roanoke, Pigg, and Nottoway rivers. Availability variables included depth (cm), bottom and mean velocity (m/s), dominant and subdominant substrate (rank category), embeddedness (rank category), and silt cover (rank category). Variables were separated by mesohabitat type (riffle, run, or pool) before analysis. Pairwise differences between mesohabitat types were examined

separately using Scheffe's multiple comparisons. I also used multivariate discriminant analysis to compare overall microhabitat availability among the three rivers.

Microhabitat use data included depth; mean velocity; bottom velocity; embeddedness; silt cover; and point, dominant, and subdominant substrates. *G*-tests with Williams' correction (Williams 1976) were used to detect habitat selection by logperch for each river via comparisons of actual habitat use with that expected if logperch used habitat randomly. Category ranges were selected such that each category was equally available in a given river; thus, categories differed among rivers. Alpha values were adjusted for multiple tests using the Dunn-Sidak correction (adjusted $\alpha=0.01$). Differences in logperch habitat use among the three rivers for each habitat characteristic were tested with analysis of variance (ANOVA) and Sheffe's multiple comparisons. Multivariate analysis of logperch habitat use in comparison to available habitat in all three rivers was examined with principal components analysis (PCA) using a correlation matrix with varimax rotation. Linearity assumptions were verified for each PCA. In addition, PCA was used to illustrate differences among rivers in habitat use by Roanoke logperch, which were quantitatively examined with multivariate analysis of variance (MANOVA) and discriminant analysis.

In addition to these analyses, I developed a logistic regression model for each river relating habitat variables to the presence of logperch (SAS® System Version 8.2, Cary, NC; Allison 1999). To obtain the most parsimonious models possible, variables used in the logistic regression, including interaction terms, were eliminated from the model using backwards selection. Variables typically were eliminated because they strongly covaried with other habitat variables or did not significantly contribute to the fit of data to the model (no or slight increase in AIC criterion or a non-significant Wald χ^2). Multicollinearity assumptions were met for each model. I verified the fit of these models by evaluating the ability of the model to predict the presence of logperch (sensitivity) from available habitat (specificity) in the data set from which the model was developed.

I used sensitivity and specificity to assess the strengths, weaknesses, and applicability of the regression models (Olden and Jackson 2001). Sensitivity measures the ability of a model to correctly identify presences (sensitivity = “# of true presences” / [“# of true presences” + “# of false absences”]). Specificity measures the ability of the model to correctly identify absences (specificity = “# of true absences” / [“# of true absences” + “# of

false presences”]). Following verification of a model for the river for which it was developed, I then examined if models developed in one river were applicable to the other two rivers where logperch occur (transferability). Each model was applied to the microhabitat data points from the other two locations, and its sensitivity and specificity was evaluated to determine the transferability of the habitat model. Overall correctness of the models was not used to assess transferability because the data sets were highly biased towards availability data points.

It should be noted that the logistic regression analysis assumes that no logperch are present in areas where available habitat was measured, which is an unlikely assumption to be met. In fact, habitat configurations occupied by logperch are a subset of available habitat. A 0.50 “cutoff” probability level for predicting the presence of logperch was not appropriate for purposes of model verification and transferability for two reasons: 1) the data do not consist of presences and absences as the model assumes, but rather presences and availability, and 2) the data set is overwhelmingly biased towards availability data points, which drive the analysis. I therefore used a cutoff value equal to the proportion of sample points for which logperch were present (Hosmer and Lemeshow 1989). This is calculated as the number of presences in the data set divided by the total number of sample points. When I verified the models using the entire range of cutoff levels (0.01 to 1 at 0.01 intervals), I found that the cutoff probabilities derived from these proportions closely approximated the probabilities that maximized model sensitivity and specificity (Hosmer and Lemeshow 1989). To verify a model, I used a cutoff value equal to the proportion of presences and availability data points for the river for which the model was developed (Roanoke River = 0.07, Pigg River = 0.04, Nottoway River = 0.03). To examine transferability, I used a cutoff value equal to the proportion of presences and availability for all rivers combined (0.047).

RESULTS

Microhabitat availability

Microhabitat availability differed among the three rivers, reflecting differences in regional characteristics, size, gradient, and human impact. The Pigg River depth was consistently shallower for all mesohabitat types ($F \geq 39.2$, $P < 0.001$, Table 1.1). Bottom

velocities were greatest for Roanoke River riffles and pools ($F \geq 3.7, P \leq 0.02$); however, bottom velocities did not vary among rivers for runs ($F = 0.30, P = 0.71$). Mean velocities in runs and riffles did not differ among rivers ($F \leq 3.1, P \geq 0.06$). For pools, mean velocities were fastest in the Roanoke River, intermediate in the Nottoway River, and slowest in the Pigg River ($F = 8.3, P < 0.001$). Substrate characteristics of pools, riffles, and runs differed among rivers, particularly silt and embeddedness (Table 1.1). Dominant substrate was largest in the Roanoke River for all mesohabitat types ($F \geq 23.7, P < 0.001$). Dominant substrate size in the Pigg and Nottoway river pools and runs did not differ. For riffles, the Nottoway River had larger dominant substrate sizes than the Pigg River ($F = 30.1, P < 0.001$). Subdominant substrate in all rivers ranged between sizes 4 (sand) and 6 (large gravel) for pools and riffles and did not differ among rivers ($F \leq 1.3, P \geq 0.27$). Subdominant substrate in Roanoke River runs was largest compared to Pigg and Nottoway river runs ($F = 12.0, P < 0.001$). Differences in embeddedness and silt cover among the three rivers were consistent and dramatic. The Nottoway River had the most exposed and least silted habitat for all mesohabitat types, while the Pigg River had the most embedded and silted habitats ($F \geq 20.3, P < 0.001$).

Discriminant analysis was used to summarize differences among rivers for all mesohabitat types and all microhabitat variables combined (Figure 1.2). This analysis corroborated univariate analyses, suggesting that the rivers differ most in depth and substrate characteristics. Canonical discriminant functions of the two axes (Table 1.2) indicated that depth and silt cover most heavily load the first axis (Figure 1.2). Plots of the confidence intervals around mean canonical scores for each river indicated that the Nottoway River was the deepest and least silted, the Roanoke River intermediate, and the Pigg River the shallowest and most silted. The second axis is loaded most heavily by dominant substrate size and depth (Table 1.2, Figure 1.2). There is little separation among rivers along the second axis; however, as the univariate analysis indicated, the Roanoke River has the largest substrate sizes (Figure 1.2). Regardless of differences among rivers, confidence intervals around mean canonical scores indicate strong overlap in microhabitat characteristics among rivers and suggested that transferability of habitat use patterns is possible.

Univariate analysis of microhabitat use

Microhabitat use by logperch reflected their use of mesohabitat types. Logperch in the Roanoke and Pigg rivers were primarily observed in runs, occasionally in riffles, and rarely in pools (Table 1.3). Differences in Roanoke logperch mesohabitat use in the Nottoway River are striking; logperch were observed primarily in pools, occasionally in runs, and rarely in riffles. Logperch observed in the Roanoke River selected deep, high velocity microhabitats with exposed, silt free gravel substrate ($G \geq 23.7$, $P < 0.001$) and did not appear to select for bottom velocities ($G = 1.3$, $P = 0.83$, Figure 1.3). Although logperch selection of depth or bottom velocity categories in the Pigg River was weak ($G \leq 10.7$, $P \geq 0.02$), patterns of habitat selection were similar to those in the Roanoke River. Logperch in the Pigg River selected fast water habitats with exposed, silt-free gravel substrate ($G \geq 17.3$, $P < 0.005$). A different pattern of selection was observed in the Nottoway River, where Roanoke logperch selected deep microhabitats with medium mean velocities and low bottom velocities ($G \geq 11.3$, $P \leq 0.01$). Logperch in the Nottoway River did not appear to select for substrate or embeddedness categories ($G \leq 10.6$, $P \geq 0.02$), but did select substrates free of silt ($G = 16.9$, $P = 0.005$).

Although logperch always selected relatively deep habitats, there were significant differences among rivers: Nottoway River logperch selected the deepest habitat, Roanoke River logperch selected intermediate depths, and Pigg River logperch selected the shallowest depths ($F = 47.5$, $P < 0.001$, Scheffe's multiple comparisons, Table 1.3, Figure 1.4). I also observed variation in the use of water velocities. Roanoke River logperch were found in faster water than logperch in the Pigg and Nottoway rivers ($F = 5.8$, $P = 0.004$). I was unable to detect differences in use of bottom velocities among the three rivers ($F = 2.4$, $P = 0.10$). In contrast, Roanoke logperch in the Roanoke, Pigg, and Nottoway rivers were remarkably consistent in their use of substrate characteristics (Table 1.3, Figure 1.5). Logperch from all three rivers were observed consistently over small to large gravel (ranks 5 and 6, $F = 0.44$, $P = 0.65$) in areas dominated by large gravel to boulders (ranks 6 through 8, $F = 2.7$, $P = 0.07$). Subdominant substrates around the point where the logperch were observed in all three rivers consisted of small to large gravel (ranks 5 and 6, $F = 0.76$, $P = 0.47$). Although there were dramatic differences among rivers in embeddedness and silt characteristics (see microhabitat availability above) and logperch mesohabitat use, I did not detect a significant difference among rivers in the embeddedness and silt cover of substrates over which logperch were

observed ($F \leq 2.1$, $P \geq 0.13$). Roanoke logperch were consistently observed over loosely embedded substrate with little to no silt cover (Figure 1.5).

Multivariate analysis of habitat use

Habitat use and availability data for the Roanoke, Pigg, and Nottoway rivers ordinated through PCA into two primary principal components (Table 1.4). The first component was loaded heavily by mean and bottom velocities, while the second component was loaded heavily by silt cover, embeddedness, and dominant substrate. These rotated axes explained 27.5 and 26.7% of the variance in the data, respectively. When factor scores for availability and habitat use locations are plotted in two-dimensional multivariate space (Figure 1.6), the first axis represents a gradient from stagnant to high-velocity habitat, while the second represents a gradient from silted, embedded, small substrates to silt free, scoured, large substrates. Polygons represent the habitat availability for each river.

PCA indicated extensive overlap in habitat availability among all three rivers, with the Roanoke River providing the highest velocities (Figure 1.6). Further, the Pigg River provides smaller, more embedded and silted substrate when compared to the Roanoke and Nottoway rivers. Logperch use a range of habitat configurations in each river, but avoid extremes along axes and areas with the slowest velocities and the most silted, embedded, and smallest substrates. Logperch locations from the three rivers along both axes overlap significantly. Axis 1 indicates that logperch in the Roanoke River range from the slowest to the fastest water, whereas Pigg and Nottoway river logperch occupy slow to intermediate velocities. This finding corroborates univariate analysis, which indicated that logperch in the Roanoke River can be found in the fastest waters (Figure 1.4). As the univariate analysis indicates, logperch from the three rivers use similar substrate configurations. However, Roanoke logperch from the Roanoke River used the widest range of substrates, taking advantage of the greater availability of exposed, large substrates in this system (Figure 1.6).

Multivariate habitat use by adult Roanoke logperch differed significantly among rivers ($F = 9.59$, Wilk's lambda = 0.29, $P < 0.001$). Further, plots of discriminant analysis scores indicated segregation among rivers in habitat use (Figure 1.7). Depth and silt cover primarily load the first discriminant axis, while the second axis is most heavily loaded by mean velocity and embeddedness (Table 1.5). The canonical scores plot corroborated

univariate analyses, indicating that rivers differ most markedly in logperch use of depth and velocities. However, this multivariate analysis also indicated that embeddedness and silt play a role in discriminating habitat use among systems. The Nottoway River and the Pigg River segregate most markedly along the first discriminant axis, indicating that Nottoway River logperch are in deeper and less silted habitats than logperch observed in the Pigg River (Figure 1.7). The Roanoke River is intermediate along this axis. As was seen with the PCA analysis, logperch in the Roanoke River appear to range into faster waters but used habitat more embedded than in the Pigg and Nottoway rivers, which overlap extensively along the second axis.

Logistic regression analysis

All three of the logistic regression models showed a nonrandom distribution of Roanoke logperch in the Roanoke, Pigg, and Nottoway rivers over available habitat configurations ($\chi^2 \geq 23.0$, $P < 0.0001$, Table 1.6). Patterns of habitat use indicated by these models follow univariate analyses. The model for the Roanoke River indicated that logperch prefer deep, fast-moving waters with large substrates and low silt cover. Further, the interaction terms indicated that logperch choice of substrate sizes and silt cover was dependent on the velocity of these habitats. This logistic model, when applied to the original Roanoke River data set, correctly explained presences far better (96%) than availability (43%, Table 1.7). The model developed for the Pigg River indicated that logperch positively associate with deep water, loosely embedded substrate, and low silt cover (Table 1.6). This model correctly classified availability more accurately than presences (79% vs. 64%, Table 1.7). The model developed for the Nottoway River indicates that logperch prefer deep, slower moving water with low silt cover and larger dominant substrates (Table 1.6). This model correctly predicted only 56.7% of logperch presences, but 83.7% of the availability data points (Table 1.7).

Model transfer

Model transferability was strongly dependent on the data source, with the Roanoke and Pigg river models showing a similar pattern of model transfer. Models developed from data collected in the Pigg and Roanoke rivers more accurately predicted logperch presences

when transferred than models developed from Nottoway River data (Table 1.7). Further, both the Roanoke and Pigg river models better predicted the presence of Roanoke logperch in the Nottoway River than the presence of logperch in each other. The Nottoway River model predicts that no logperch can be found in the Pigg River and only a few logperch can be found in the Roanoke River. This trend is reversed when examining the accuracy of transferred models in identifying available habitat. The Roanoke and Pigg river models better predicted availability for each other (81% and 41%, respectively) than they did availability for the Nottoway River (29% and 16%, respectively).

DISCUSSION

Habitat use patterns and habitat availability

Analyses of Roanoke logperch habitat use in the Roanoke, Pigg, and Nottoway river systems indicated that habitat selection and use patterns differed among rivers; however, commonalities give insight into factors limiting distributions of Roanoke logperch. Although most descriptions of logperch habitat use thus far have been based on depth, velocity, and mesohabitat preferences (Burkhead 1983, Jenkins and Burkhead 1993), logperch are not consistent in their use of velocity and depth characteristics and their use of different mesohabitat types in the three rivers. This indicates that habitat descriptions based on these characteristics are not appropriate for transfer of habitat use patterns between systems.

Despite differences in use of depths, velocities, and mesohabitat, Roanoke logperch were remarkably consistent in their use of substrate characteristics. This consistency indicates that availability of suitable substrate is a critical feature of logperch habitat, and adult logperch can occupy a variety of depths, velocities, and mesohabitats to accommodate substrate requirements. This requirement may be due to the unique feeding strategy of logperch. By flipping small rocks and debris to feed on exposed insects (Burkhead 1983, Jenkins and Burkhead 1993), logperch may rely on the availability of small, loosely embedded substrate. Consistency in the use of substrate types over different stream conditions was seen in reticulate sculpin (*Cottus perplexus*) selection of nesting sites (Bateman and Li 2001). In this case and in the case of the Roanoke logperch, the characteristics of the substrate can be mechanistically linked to the behavior and life history

requirements of the species. Use of habitat features or configurations that can be linked to critical aspects of the life history of a study species seem more likely to transfer over a range of ecological conditions.

PCA indicated that logperch in the Roanoke and Pigg rivers select the fastest-water habitats available. Fast-velocity habitat similar to what logperch use in the Roanoke River is available in the Nottoway River; yet logperch in this system select intermediate velocities. Low silt loads in Nottoway River pools may enable logperch to forage and thrive in these habitats. Unlike pools in the Roanoke and Pigg rivers, Nottoway River pools have substrate characteristics that correspond closely with logperch preferences. Further, large woody debris, uncommon in the Roanoke and Pigg rivers, is abundant in pools in the Nottoway River (Rosenberger and Angermeier 2002) and can provide shelter from predators and a source of food (Angermeier 1985). Use of low velocity habitats in the Roanoke and Pigg rivers may not be an option for Roanoke logperch because of excessive silt loads and reduced woody debris in the two systems. Logperch in the Pigg and Roanoke rivers may be experiencing higher energetic costs of foraging because they must navigate fast water to forage (Fausch and White 1981, Fausch 1983).

Habitat model transfer

Logistic regression models showed a nonrandom distribution of Roanoke logperch in the Roanoke, Pigg, and Nottoway rivers. Variables important in each model followed habitat selection patterns observed in univariate analyses. The relative ability of models to predict presences and absences of logperch (sensitivity and specificity) provided more insight into the performance of each model. The Nottoway River model performed well in predicting available habitat (specificity) but poorly predicted presences (sensitivity) in the other two systems. The Pigg and Roanoke river models more accurately predicted presences in each other than in the Nottoway River system but did not perform as well as the Nottoway River model in predicting available habitat. Model transfer was weak among rivers, indicating that, if possible, separate models for each river system should be used for the management of this species.

Limitations in the approach to data collection may have contributed to weak model transfer and differences between rivers in model sensitivity and specificity. First, my

methods produced a model that was heavily biased towards habitat availability. Logistic regression treated availability data points as absences, while, in actuality, presences are nested within available habitat. This weakened the conclusiveness of the models. For most ecological data, absence information is less reliable than presence (Bayley and Peterson 2001). Other statistical approaches to modeling may be applied in these cases that can incorporate probability of detecting the species in different habitat types. Unfortunately, that information is not available in this study. Second, each model reflects habitat availability for the river system in which it is developed. Its predictive power is weakened in systems with available habitat configurations that range outside the data set on which the original model was based.

PCA performed better than logistic regression for prediction of suitable locations for Roanoke logperch in the three rivers, and may prove a better tool for examining the suitability of habitat configurations for a target species in an unsampled river. This analysis is not based on the strength of logperch selection patterns for a few ecological variables, but rather the location of habitat use and availability for all correlated variables in multivariate space. This allows the analysis to perform well with nested data sets and among rivers for which limiting factors and the range of habitat configurations differ. Leftwich et al. (1997) also found PCA more useful than logistic regression for predicting optimal habitat among systems.

Poor model transfer may also reflect variation among rivers in factors used by logperch to select habitat. My analysis indicated a relationship between the models' sensitivity and specificity and human impact on the systems (i.e., silt load). The logistic model based on data collected from the highly impacted Pigg River did well in predicting the presence of logperch in both the moderately impacted Roanoke River and relatively pristine Nottoway River. The model based on data collected from the Nottoway River performed poorly in the other two rivers, predicting only one correct presence in the Roanoke River and no logperch in the Pigg River. This trend is reversed for model specificity, with the Nottoway River model performing the best in predicting available habitat. This pattern may be explained by differences among rivers in factors limiting the distribution of Roanoke logperch. A particular variable such as silt cover or embeddedness only appears as a limiting distribution when its values cluster near the limits of the range of use of the target species.

These factors therefore rank in different orders of importance among river systems, which confounds the transferability of habitat models created with logistic regression (also see Leftwich et al. 1997). Selectivity for silt-free, loosely embedded substrate was stronger in the Pigg and Roanoke rivers, which have less of this type of habitat available. The high availability of loosely embedded, silt-free substrate in the Nottoway River weakens the apparent strength of this selection, indicating that this is not a limiting factor in this river. Consequently, logperch presences are over-predicted in the Nottoway River when the Pigg or Roanoke river models are transferred.

It is difficult to gauge to what extent poor transferability is a result of data collection limitations or biological characteristics of the Roanoke logperch. Poor transferability of microhabitat use models has been observed in other species that occupy a variety of mesohabitat types (Freeman et al. 1997), suggesting that logperch characteristics may confound model transfer. Roanoke logperch can occupy a variety of depths, velocities, and mesohabitats while strongly selecting substrate characteristics. Substrate characteristics do not neatly stratify along gradients of depth, velocity, or mesohabitat types (Vadas and Orth 1998). Riffle specialists that neatly stratify along depth and velocity gradients may be more likely to show consistency in microhabitat use between river systems (Freeman et al. 1997). Further, my analysis suggests that use of a habitat feature that can be mechanistically linked to life history requirements of the species should improve model transfer. In the case of the Roanoke logperch, use of depth and velocity characteristics in the model only confounded model transfer, while use of substrate remained consistent between systems. Future studies should emphasize patterns of model transferability in relation to mesohabitat preferences and specificity of target species and relate models to life history characteristics of the target species. I expect model transfer to be more successful for mesohabitat specialists than mesohabitat generalists.

Restoration, conservation, and monitoring programs for threatened and endangered species can use habitat model transfer to identify areas suitable for reintroduction or to predict negative or positive consequences of management or human activity. However, results of my study suggests that models should be transferred only with caution, particularly for substrate specialists and mesohabitat generalists such as the Roanoke logperch that do not neatly stratify along depth or velocity gradients. This study also suggests that transfer will be

weak among systems that differ in habitat availability and human impact because the importance of habitat features for the target species will vary among these systems. Modeling techniques that rely on a target species' strong selection of a few habitat variables may not be as useful as techniques that examine the use of multiple strongly correlated habitat variables regardless of the strength of habitat selection.

Conclusions

The consistent use of silt-free, loosely embedded gravel in all rivers strongly suggests that substrate features are most important for adult Roanoke logperch. Although descriptions of Roanoke logperch habitat use previous to this study have been primarily based on depth, velocity, and mesohabitat preferences (Burkhead 1983, Jenkins and Burkhead 1993), comparison between logperch populations indicate that habitat models and descriptions based on these characteristics are not appropriate for transfer among rivers. This species' strong and consistent selection of exposed, silt-free gravel substrate is probably due to its foraging strategy of flipping gravel and small debris to search for small insects (Burkhead 1983, Jenkins and Burkhead 1993). Use of low velocity habitats in the Roanoke and Pigg rivers may not be an option for logperch because of heavy silt loads.

Effective strategies for logperch conservation may differ among rivers. Preventative, anti-degradation measures to preserve the existing population are appropriate for the Nottoway River. Management programs on the Roanoke and Pigg rivers should focus more on restoration. In agricultural areas, livestock exclusion, streambank reconstruction and enhancement of riparian zones should reduce sedimentation that impacts the quality of logperch habitat. In urban areas, effective management for logperch will involve riparian restoration and enforcement of laws intended to prevent sedimentation during construction activities (i.e. maintenance of silt fences). Any activity that reduces the competency of the channel (i.e. channel straightening) will impact logperch habitat. Scouring flow through a natural channel may enhance habitat quality through removal of fine sediments. Management actions selected to promote logperch conservation should be carefully designed and monitored to ensure effectiveness.

This study indicates several approaches that may increase the success of habitat studies of threatened or endangered species that occupy multiple rivers. First, a comparative

study of habitat use patterns between these systems can suggest generalized habitat requirements for the target species and give insight to what habitat features are most important to its distribution. This could contribute to more informed management plans with efficient allocation of resources. Selection of a particular habitat characteristic in one system does not warrant concluding that this feature generally limits the distribution of the target species. However, if a habitat feature is used consistently regardless of available habitat, it is probably important to that species. Second, if knowledge is constrained to one river, identifying a mechanistic link between habitat use patterns and the biology of the target species may assist managers in isolating habitat variables important to the species in all rivers within its range. Third, models may transfer effectively between rivers that impose similar constraints whether or not they are based on actual limiting factors for the study species. Finally, logistic regression models may not be the best choice for identifying suitable habitat in unsampled systems. Univariate analyses or ordination techniques that incorporate multiple variables may be a better approach to selecting areas suitable for the target species.

Table 1.1 Summary of microhabitat characteristics (mean \pm standard deviation) of pools, riffles, and runs in the Roanoke, Pigg, and Nottoway rivers. *Indicates a significant difference at the 0.05 level (ANOVA). Underlines indicate no significant difference between river pairs (Sheffe's multiple comparisons, $\alpha = 0.05$).

POOL CHARACTERISTICS	Roanoke River (R)	Pigg River (P)	Nottoway River (N)	F	P	
Depth (m)	75.7 \pm 45.1	38.8 \pm 23.3	84.9 \pm 35.9	82.4	<0.001 *	R P N
Bottom velocity (m/s)	0.06 \pm 0.24	0.03 \pm 0.05	0.04 \pm 0.09	3.7	0.02 *	R P N
Mean velocity (m/s)	0.21 \pm 0.45	0.10 \pm 0.08	0.15 \pm 0.15	8.3	<0.001 *	R P N
Dominant substrate (mean rank)	5.9 \pm 2.5	4.6 \pm 2.2	4.7 \pm 2.2	23.7	<0.001 *	R P N
Subdominant substrate (mean rank)	4.8 \pm 1.9	4.4 \pm 2.2	4.6 \pm 2.4	1.3	0.27	<u>R P N</u>
Embeddedness (mean rank)	2.5 \pm 1.4	1.8 \pm 0.90	3.5 \pm 1.3	110	<0.001 *	R P N
Silt (mean rank)	2.4 \pm 1.5	1.4 \pm 0.80	3.4 \pm 1.5	116	<0.001 *	R P N
N	270	147	401			
RUN CHARACTERISTICS						
Depth (m)	35.8 \pm 21.16	24.8 \pm 10.5	50.7 \pm 24.0	61.5	<0.001 *	R P N
Bottom velocity (m/s)	0.08 \pm 0.16	0.08 \pm 0.09	0.07 \pm 0.13	0.30	0.71	<u>R P N</u>
Mean velocity (m/s)	0.25 \pm 0.31	0.19 \pm 0.14	0.28 \pm 0.33	3.1	0.06	<u>R P N</u>
Dominant substrate (mean rank)	7.0 \pm 1.7	5.5 \pm 1.6	5.4 \pm 2.2	43.3	<0.001 *	R P N
Subdominant substrate (mean rank)	5.9 \pm 1.6	5.2 \pm 1.7	5.1 \pm 2.1	12.0	<0.001 *	R P N
Embeddedness (mean rank)	3.3 \pm 1.3	3.1 \pm 1.0	3.9 \pm 1.3	20.3	<0.001 *	<u>R P N</u>
Silt (mean rank)	3.4 \pm 1.4	3.1 \pm 1.3	4.3 \pm 1.2	42.7	<0.001 *	R P N
N	223	87	316			
RIFFLE CHARACTERISTICS						
Depth (m)	26.2 \pm 16.3	16.0 \pm 8.9	34.3 \pm 21.3	39.9	<0.001 *	R P N
Bottom velocity (m/s)	0.16 \pm 0.30	0.11 \pm 0.15	0.08 \pm 0.19	5.8	0.003 *	R P N
Mean velocity (m/s)	0.40 \pm 0.44	0.25 \pm 0.23	0.37 \pm 0.48	2.5	0.10	<u>R P N</u>
Dominant substrate (mean rank)	7.7 \pm 1.0	6.1 \pm 1.5	6.9 \pm 2.3	30.1	<0.001 *	R P N
Subdominant substrate (mean rank)	5.7 \pm 1.6	5.5 \pm 1.6	5.6 \pm 2.0	0.24	0.79	<u>R P N</u>
Embeddedness (mean rank)	3.7 \pm 1.1	3.3 \pm 1.2	4.3 \pm 1.1	27.7	<0.001 *	R P N
Silt (mean rank)	4.0 \pm 1.4	3.4 \pm 1.4	4.5 \pm 1.0	30.5	<0.001 *	R P N
N	202	105	220			

Table 1.2 Canonical discriminant functions of a discriminant analysis comparing microhabitat availability among the Roanoke, Pigg, and Nottoway rivers (Figure 2).

Microhabitat characteristics	Axis 1	Axis 2
Depth	0.65	0.56
Bottom velocity	-0.28	0.27
Mean velocity	-0.09	-0.54
Dominant substrate size	-0.32	0.95
Subdominant substrate size	-0.22	0.12
Embeddeness	0.50	-0.37
Silt Cover	0.71	0.19

Table 1.3 A summary of habitat characteristics of locations where adult Roanoke logperch were observed during snorkeling surveys in the Roanoke, Pigg and Nottoway rivers.

	<i>Roanoke River</i>	<i>Pigg River</i>	<i>Nottoway River</i>
% Total logperch observed in			
Pools	11 %	0 %	69 %
Riffles	22 %	36 %	21 %
Runs	67 %	64 %	10 %
Depth (cm), SD	51.5 ± 12.8	32.0 ± 10.4	84.2 ± 27.8
Mean velocity (m/s), SD	0.59 ± 0.68	0.30 ± 0.15	0.20 ± 0.17
Bottom velocity (m/s), SD	0.15 ± 0.30	0.11 ± 0.09	0.02 ± 0.09
Point Substrate (mean rank), SD	5.8 ± 1.6	5.4 ± 0.5	5.1 ± 2.0
Dominant Substrate (mean rank), SD	7.2 ± 1.6	6.4 ± 0.8	6.1 ± 2.1
Subdominant Substrate (mean rank), SD	5.4 ± 1.6	5.9 ± 1.1	5.2 ± 2.2
Embeddedness (mean rank), SD	3.8 ± 1.1	4.0 ± 0.9	4.2 ± 1.0
Silt (mean rank), SD	4.0 ± 1.2	4.0 ± 1.2	4.5 ± 0.7
N	54	14	39

Table 1.4 Summary of PCA of logperch habitat use and habitat availability for the Roanoke, Pigg, and Nottoway rivers (see Figure 6) and loadings of seven habitat variables on the first two principal components and percent of total variance explained by each component.

	Axis 1	Axis 2
Eigenvalue	2.69	1.11
% variance explained	27.5	26.7
Component Loadings:		
Bottom velocity	0.88	0.03
Mean velocity	0.85	0.19
Silt Cover	0.50	0.63
Embeddedness	0.40	0.68
Dominant Substrate	0.05	0.68
Subdominant Substrate	-0.08	0.06
Depth	-0.13	-0.32

Table 1.5 Canonical discriminant functions for discriminant analysis of logperch habitat use for the Roanoke, Pigg, and Nottoway rivers (see Figure 7).

Canonical Discriminant Functions	1	2
Depth	1.09	0.31
Bottom velocity	-0.11	0.12
Mean velocity	-0.34	0.73
Point substrate	0.05	0.16
Dominant Substrate	-0.32	0.33
Subdominant Substrate	-0.15	0.39
Embeddedness	-0.11	-0.78
Silt Cover	0.86	0.33

Table 1.6 Summary of logistic regression models used to estimate probability of presence of Roanoke logperch in microhabitat locations in the Roanoke, Pigg, and Nottoway rivers, Virginia. Parameter estimates are maximum-likelihood estimates, and significance of each variable is based on Wald χ^2 . Significance of each model is based on a χ^2 of the -2 log-likelihood statistic.

Roanoke River Model		($\chi^2 = 38.5$, df = 6, P < 0.0001)		
Variable	Parameter Estimate	χ^2	df	P
Intercept	-7.0	31.2	1	< 0.0001
Depth (cm)	0.01	7.1	1	0.008
Mean velocity (m/s)	8.6	10.8	1	0.001
Dominant substrate (rank)	0.25	4.0	1	0.04
Silt (rank)	0.42	6.7	1	0.01
Average velocity x Dominant substrate	-0.49	6	1	0.15
Average velocity x Silt	-0.84	3.8	1	0.05

Pigg River Model		($\chi^2 = 23.0$, df = 3, P < 0.0001)		
Variable	Parameter Estimate	χ^2	df	P
Intercept	-8.3	31.9	1	<0.0001
Depth (cm)	0.04	6.7	1	0.009
Embeddedness (rank)	0.74	3.5	1	0.06
Silt (rank)	0.46	1.8	1	0.18

Nottoway River Model		($\chi^2 = 29.6$, df = 4, P < 0.0001)		
Variable	Parameter Estimate	χ^2	df	P
Intercept	-9.2	33.3	1	< 0.0001
Depth (cm)	0.02	17.5	1	< 0.0001
Mean velocity (m/s)	-1.3	1.8	1	0.18
Dominant substrate (rank)	0.14	2.6	1	0.11
Silt (rank)	0.88	9	1	0.003

Table 1.7 The sensitivity and specificity of logistic regression models developed to predict the presence of Roanoke logperch in the Roanoke, Pigg, and Nottoway rivers. Underlined values indicate model verification. The remaining values indicate the transferability of models from one river to the next.

Data Source for logistic regression models

Sensitivity/ Specificity

Models transferred to:	Roanoke River	Pigg River	Nottoway River
Roanoke River data sets	<u>0.93/ 0.43</u>	0.82/ 0.41	0.02/ 0.98
Pigg River data sets	0.79/ 0.81	<u>0.64/ 0.79</u>	0/ 1
Nottoway River data sets	0.97/ 0.29	1/ 0.16	<u>0.57/ 0.84</u>

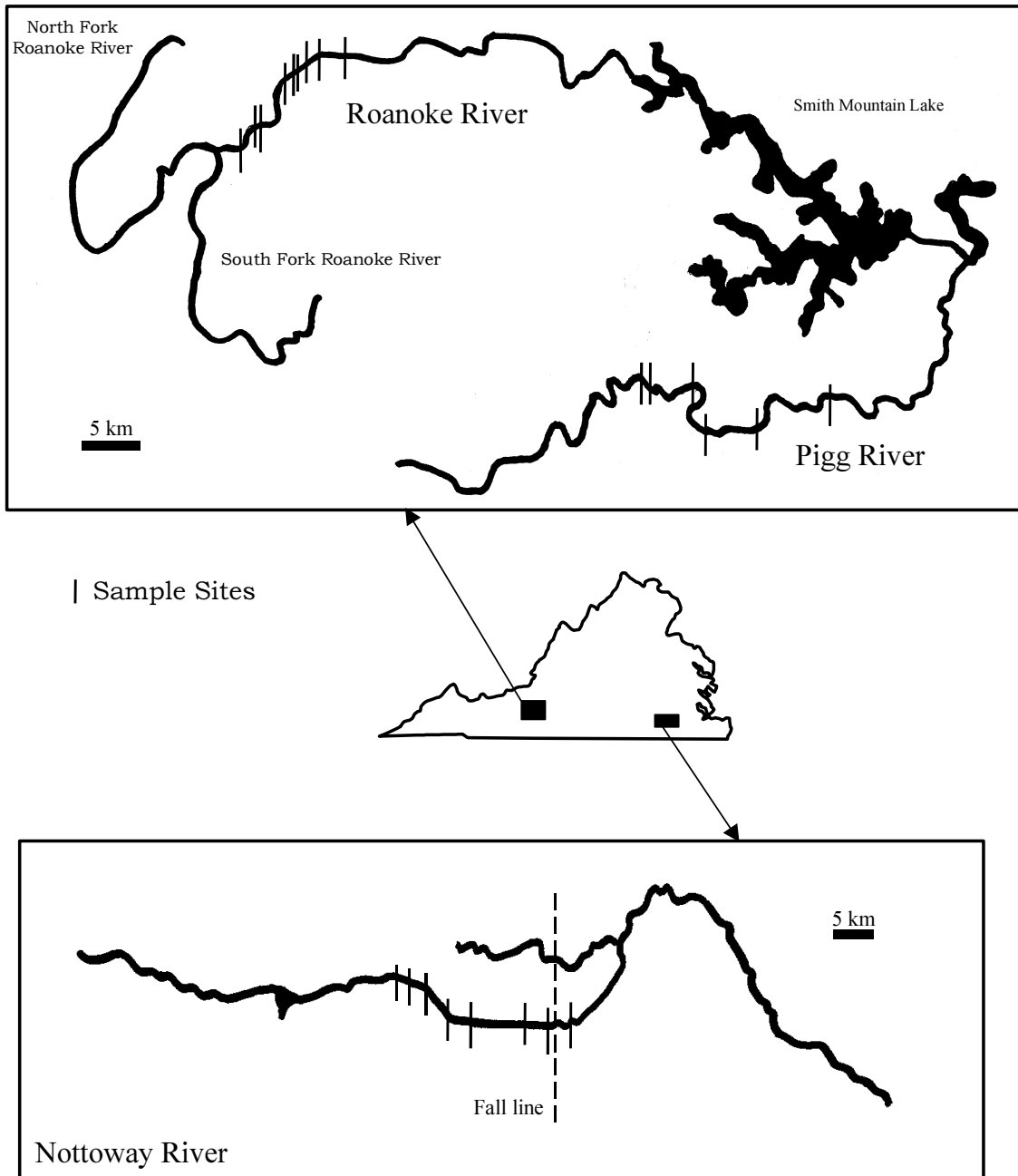


Figure 1.1 Map of the Roanoke, Pigg, and Nottoway rivers, Virginia, indicating sites selected for snorkeling surveys.

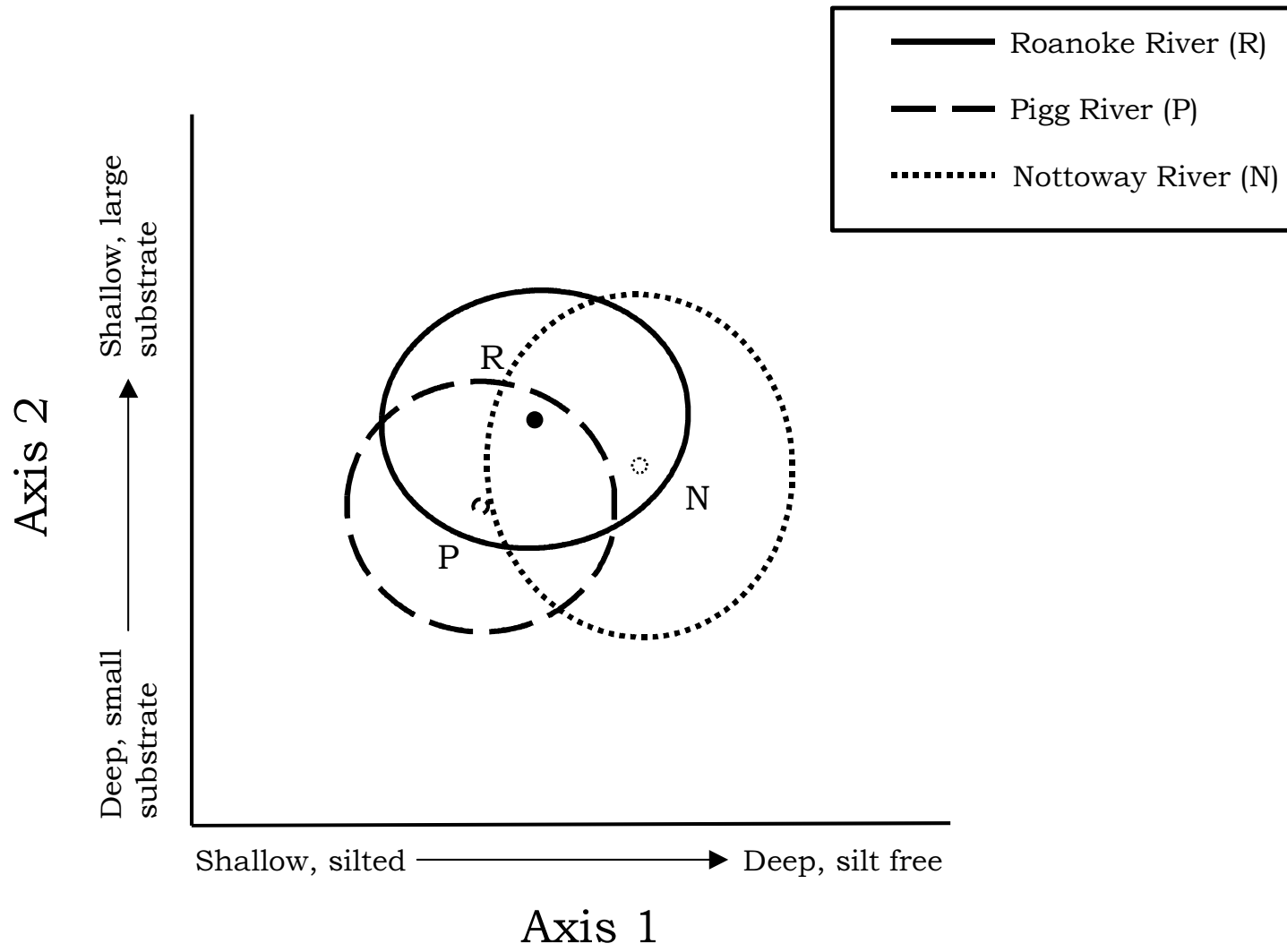


Figure 1.2 Discriminant analysis of microhabitat availability measurements for the Roanoke, Pigg, and Nottoway rivers, Virginia. Axis labels are based on canonical discriminant functions of Factor 1 and 2. Circles represent 95% confidence intervals around the mean canonical value for each river.

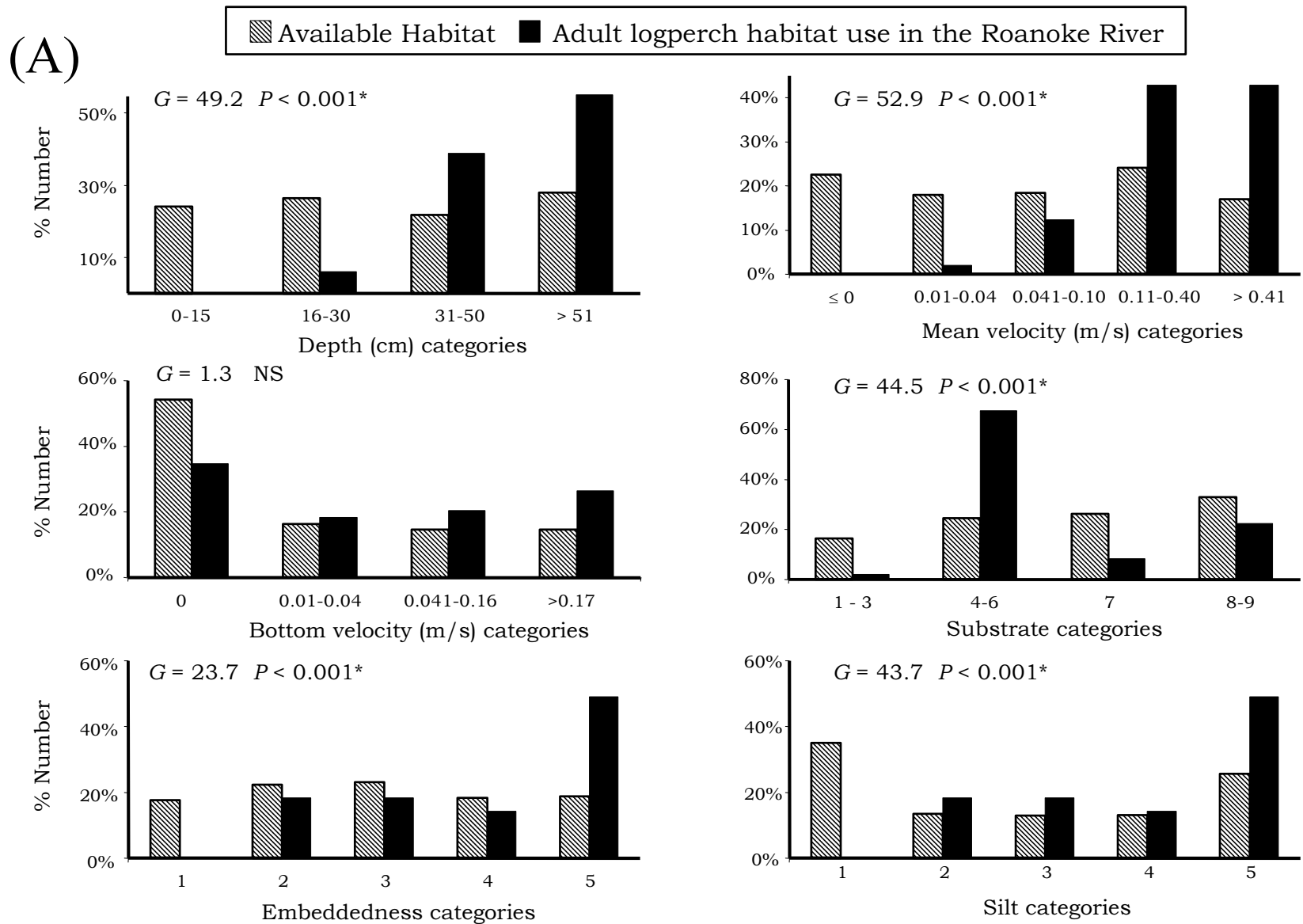
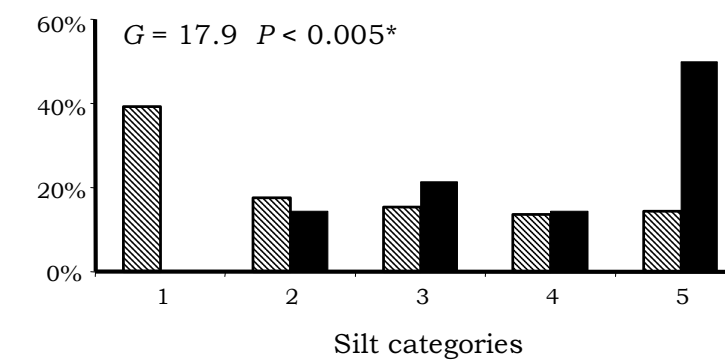
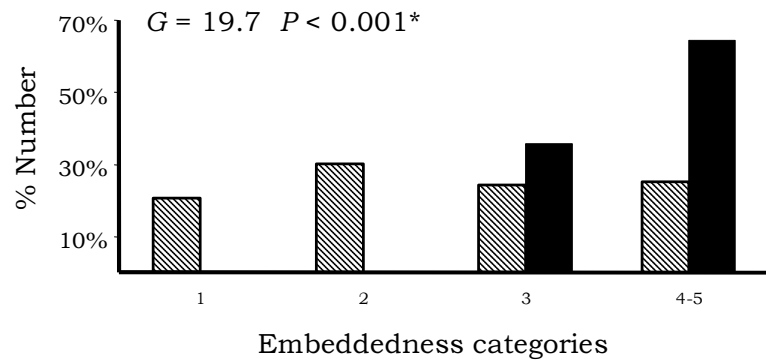
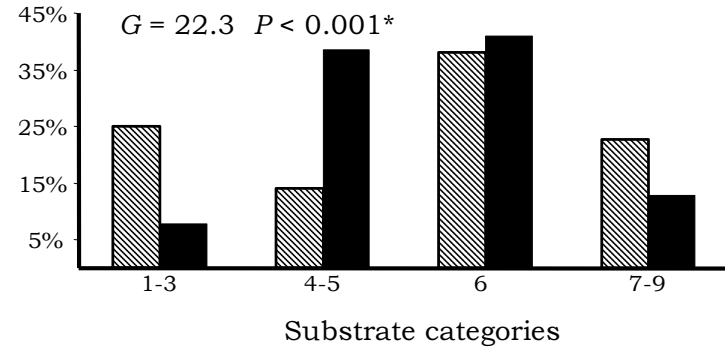
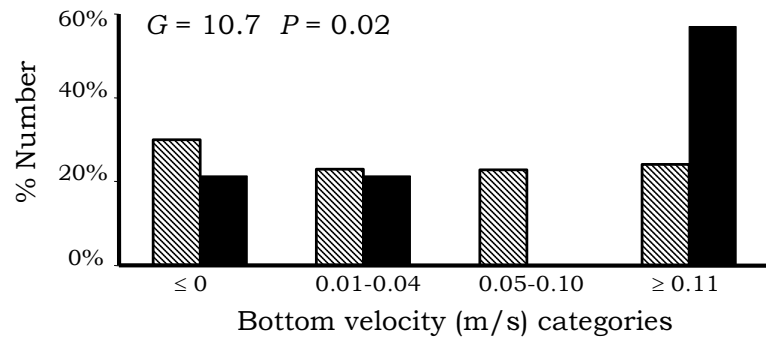
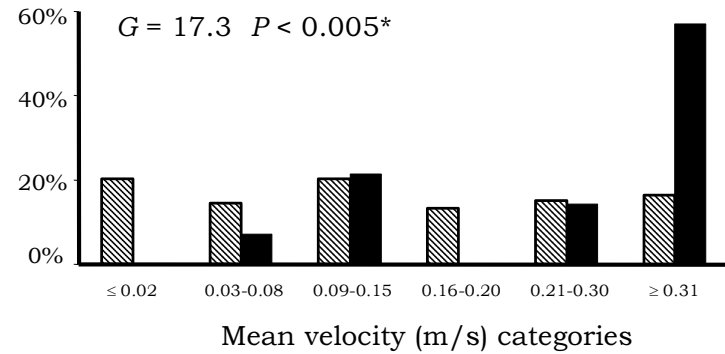
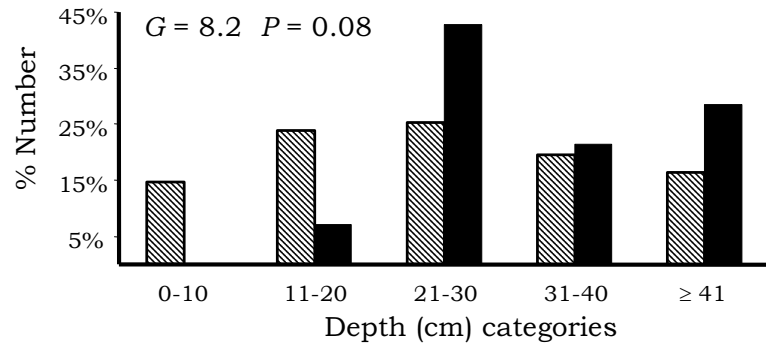


Figure 1.3 Proportional abundance of available habitat and proportional occurrence of adult logperch in habitat categories in the Roanoke (A), Pigg (B), and Nottoway (C) rivers, Virginia. Data were collected during summer sampling. * indicates a significant G -test at the 0.01 level (Dunn-Sidak correction for multiple tests). Significance indicates non-random selection.

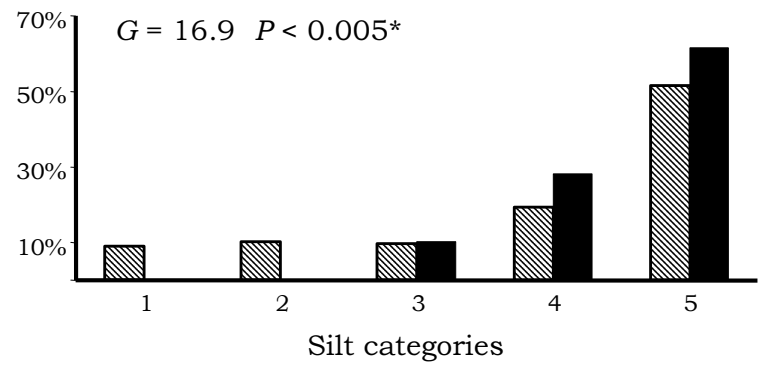
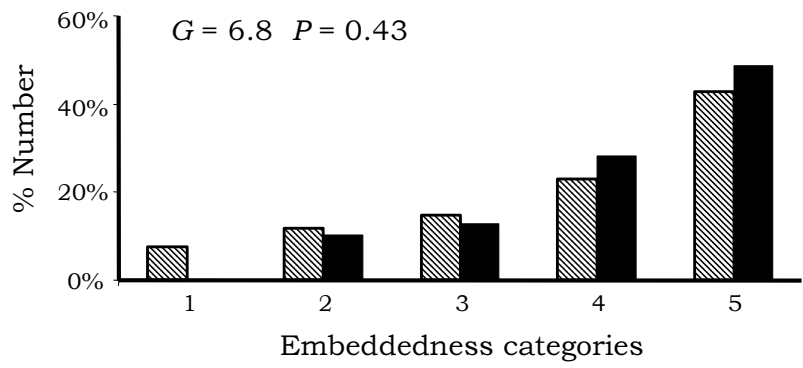
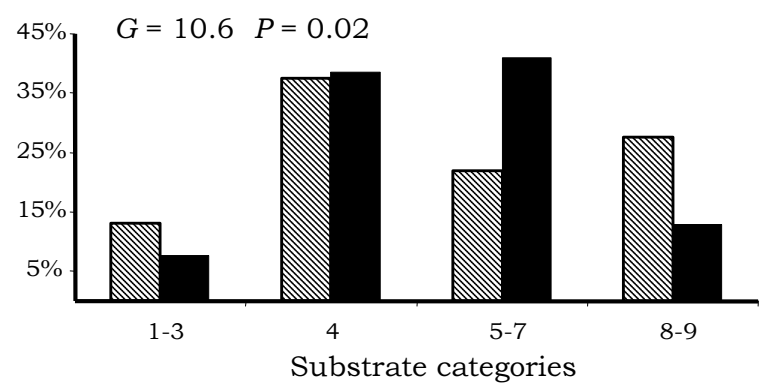
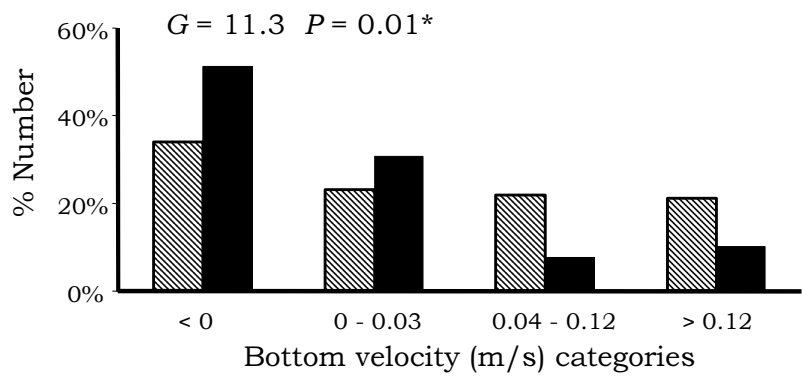
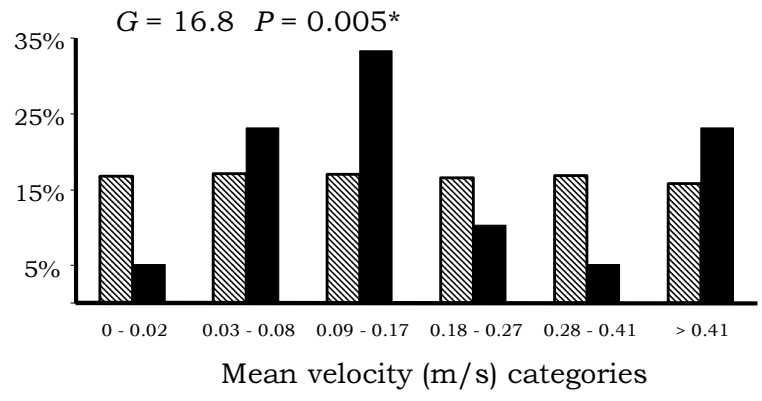
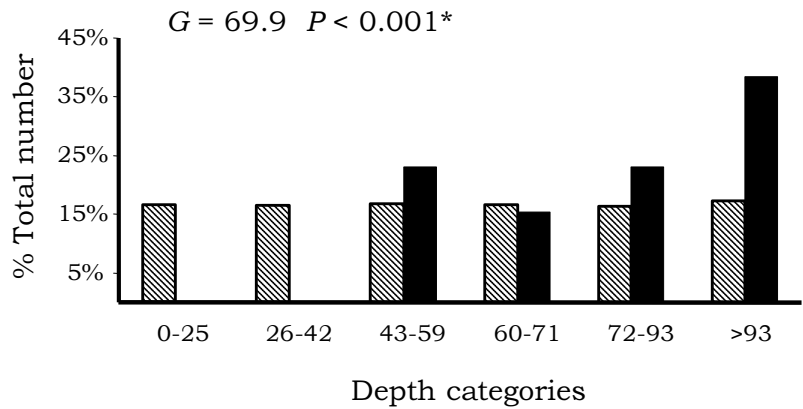
(B)

▨ Available Habitat ■ Adult logperch habitat use in the Pigg River



(C)

▨ Available Habitat ■ Adult logperch habitat use in the Nottoway River



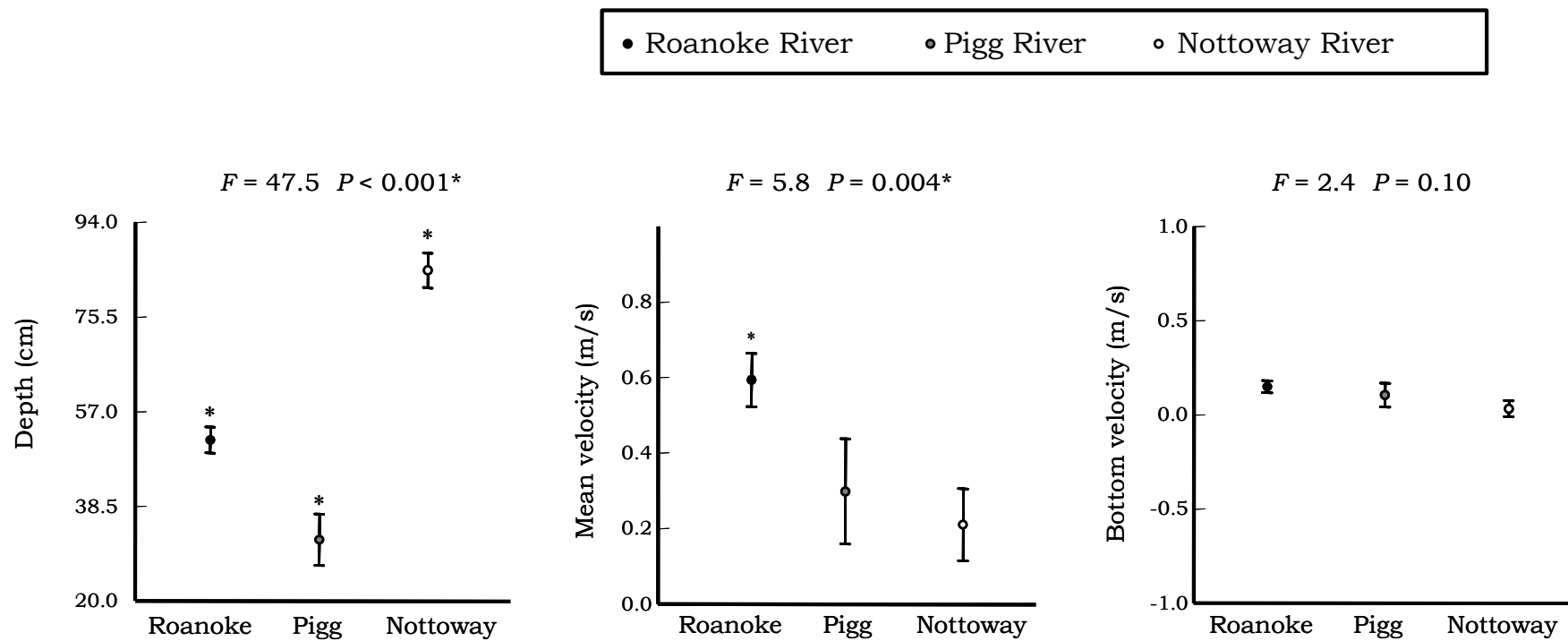


Figure 1.4 Mean habitat use (depth, mean velocity, and bottom velocity) of adult Roanoke logperch observed in the Roanoke, Pigg, and Nottoway Rivers, Virginia. *Indicates a significant difference at the 0.05 level (ANOVA, Scheffe's multiple comparisons).

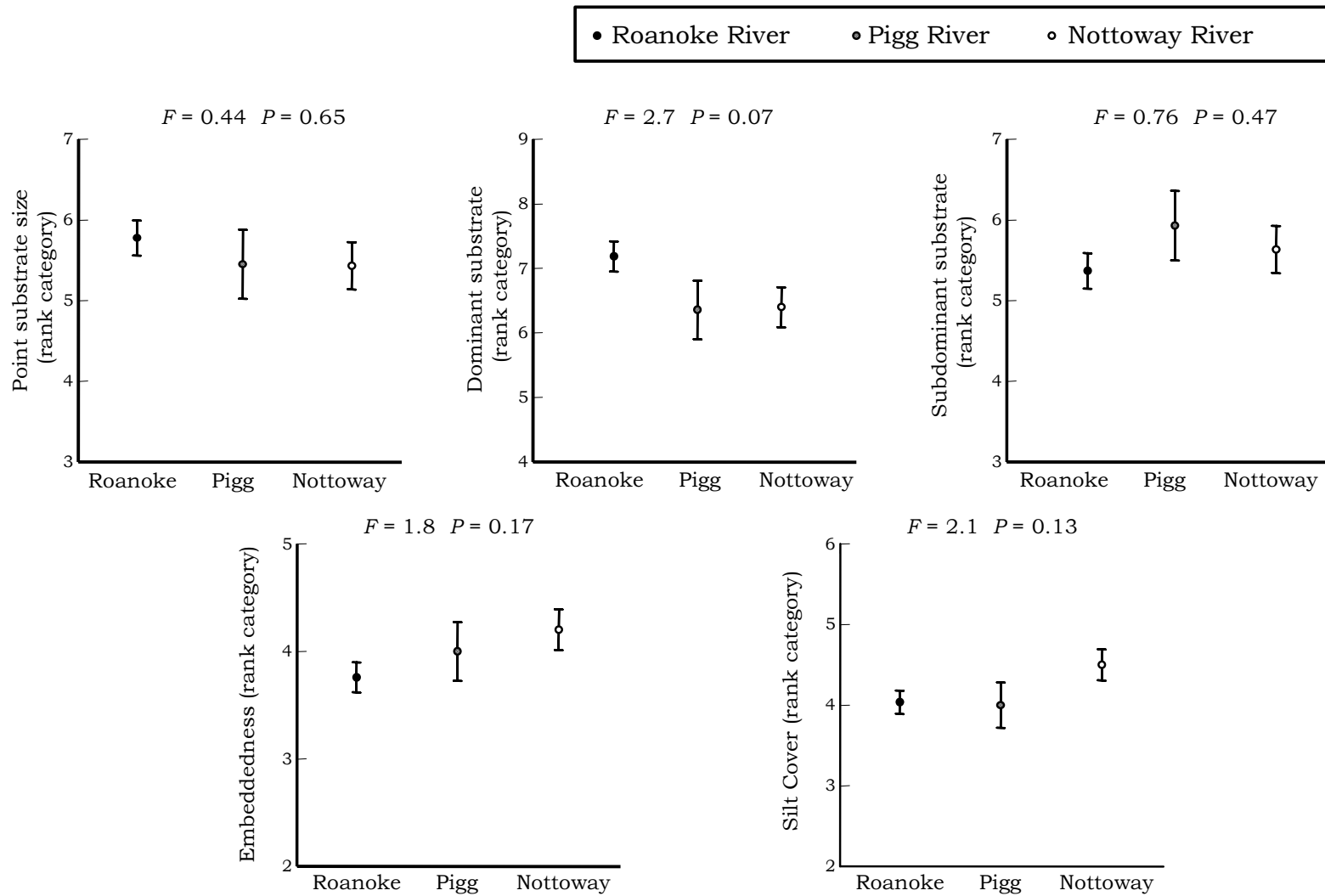


Figure 1.5 Mean use of substrate characteristics by adult Roanoke logperch observed in the Roanoke, Pigg, and Nottoway rivers, Virginia.

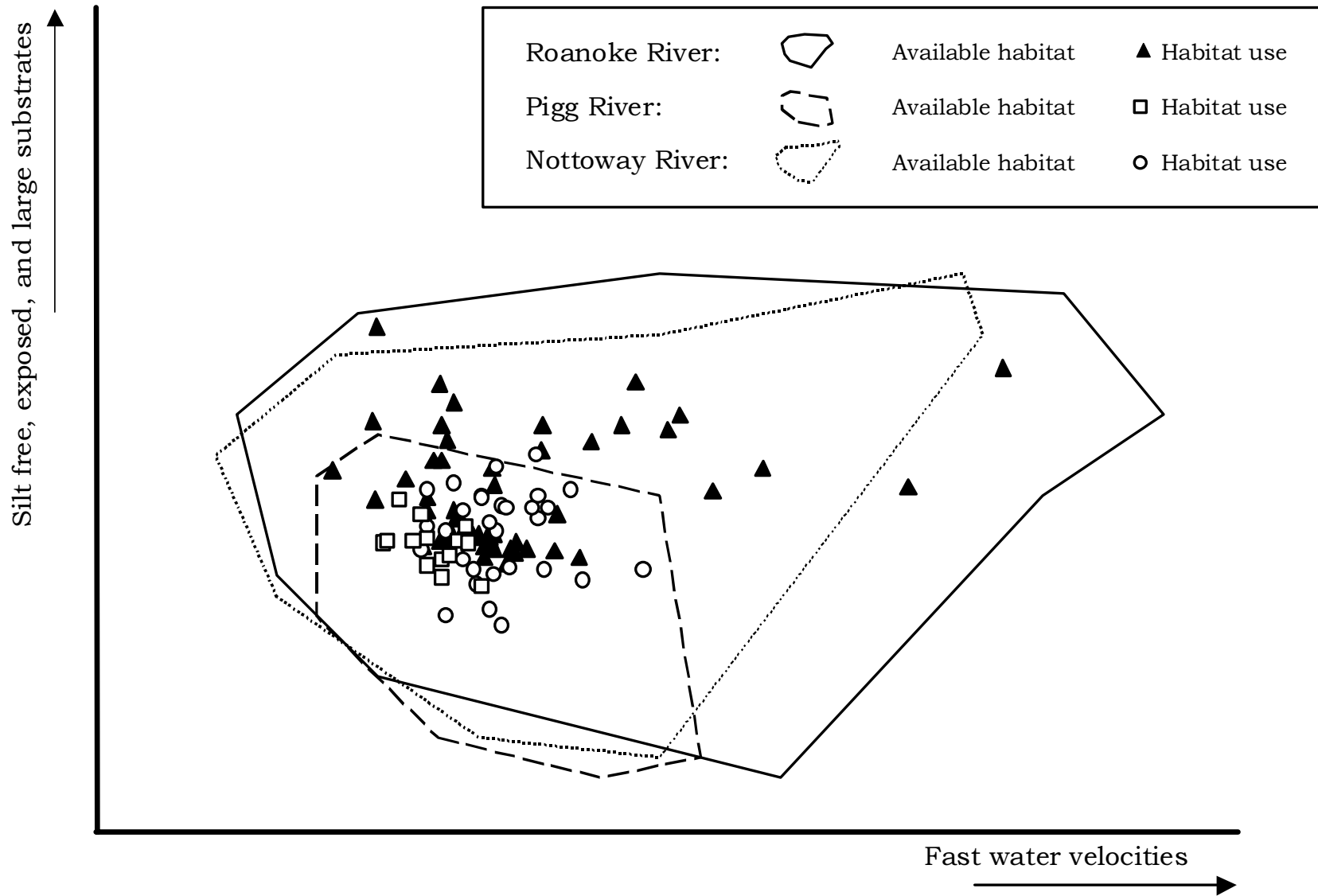


Figure 1.6 A graphical presentation of principal component scores for microhabitat availability and use by Roanoke logperch in the Roanoke, Pigg, and Nottoway rivers, Virginia. The polygons circumscribe the area representing available microhabitat.

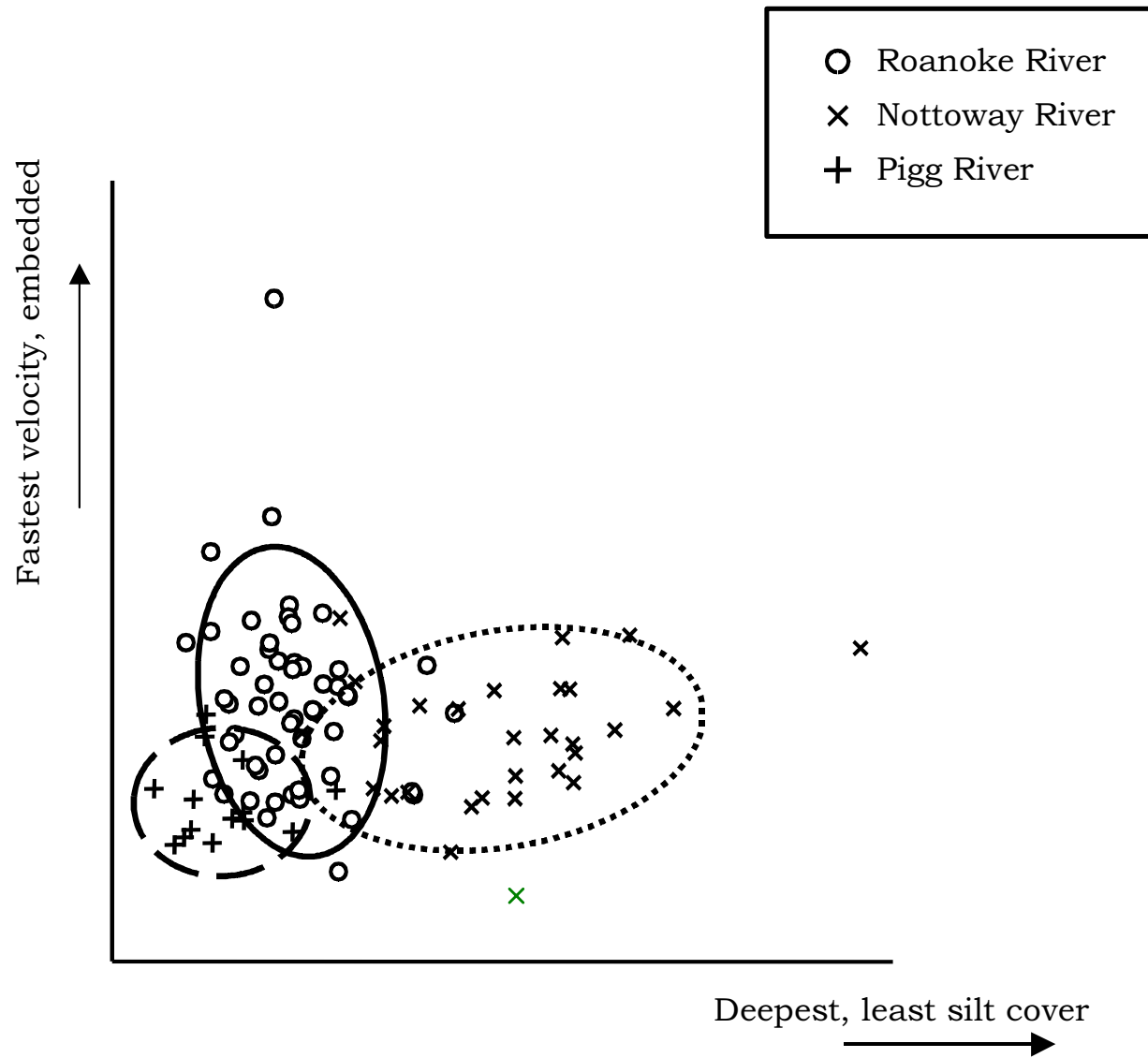


Figure 1.7 Discriminant analysis of habitat use by Roanoke logperch in the Roanoke, Pigg, and Nottoway rivers. Ellipses around data points are 95% confidence intervals around mean canonical scores.

Chapter 2. Transferability of micro- and meso-habitat associations of Roanoke logperch (*Percina rex*) between the Roanoke and Nottoway rivers

INTRODUCTION

Understanding the spatial distributions of species in relation to environmental features is central to advancing the fields of fish ecology and conservation. Discontinuities in a species' distribution throughout its range are likely regulated by environmental suitability and dispersal pathways for colonists (Angermeier et al. 2002). These factors can be viewed hierarchically, from large regional patterns to local patterns (Frissel et al. 1986, Tonn et al. 1990, Angermeier and Winston 1998, Angermeier et al. 2002). A hierarchical approach to describing habitat associations for fish species may reveal both large- and small-scale factors that are important in determining a species' distribution, dynamics, and recovery from disturbance (Wiens 1989, Menge and Olson 1990, Reice et al. 1990, Watson and Hillman 1997).

Studies conducted at multiple scales are powerful tools for advancing the understanding of what limits the distribution of a species in a stream or system. Different key determinates of distributional patterns often emerge at different scales of investigation. Multiscale studies also can illustrate limitations in the data and assist in avoiding errors of interpretation (Frost et al. 1988, Welsh and Perry 1998). A multi-scale approach additionally can establish cause-response linkages between different scales and provide insight into mechanistic links between fish distributions and the environment, leading to development of more informed management plans (Imhof et al. 1996, Lohr and Fausch 1997, Labbe and Fausch 2000). For example, site-specific management strategies may prove effective for a species that is limited by suitable microhabitat patches but are unlikely to restore a threatened species whose range has become restricted by large-scale land use patterns or the system-wide invasion of a nonnative species. Further, even site-specific problems (e.g. channel instability) may require watershed-scale treatment (e.g. runoff retention).

Models of species' habitat associations typically assume that observed habitat use: 1) reflects preferences, 2) optimizes fitness, and 3) is characteristic of a species and, 4)

therefore, should be transferable between populations in different streams (Angermeier 1987, Baltz et al. 1987, Bozek and Rahel 1992). Transferable habitat models are particularly useful for conservation purposes because they can identify suitable habitat in areas that are poorly surveyed, identify areas suitable for reintroduction, justify protection of areas that are not occupied, and indicate distributional limiting factors (Angermeier et al. 2002). Further, a single, transferable habitat model would obviate the need for developing costly site-specific habitat models. Unfortunately, the predictive power of many habitat models has been limited to the locality in which they were originally developed, and models have been transferred from one situation or system to another with mixed success (Bowlby and Roff 1986, Angermeier 1987, Layher et al. 1987, Hubert and Rahel 1989, Rabeni and Sowa 1996, Leftwich et al. 1997, Dunham et al. 2002). Presumably, habitat models that are not transferable among populations do not reflect actual preferences related to the fitness of the species. Transfer can also be confounded by variation in the availability of optimal or preferred habitat among locations.

For this study, I use a conceptual framework based on the three assumptions of habitat modeling studies. Ideally, controlled laboratory experiments could be used to examine whether habitat use of a species actually reflects preferences, optimizes fitness, and is consistent across a variety of conditions. If this type of experiment is not feasible due to logistic or ethical constraints or to scarcity of the study species, comparative, hierarchical field studies can lend insight. I use a hierarchical approach to pinpoint invariant distributional patterns and consistently occupied habitat configurations that behave similarly across populations of a species. Further, I relate these patterns to the species' life history characteristics. This approach can indicate actual habitat preferences and limiting factors that are related to the fitness of the study species. Further, I use a hierarchical, multi-scale approach to habitat modeling to increase the likelihood of creating a transferable, broadly applicable model (Poff 1997, Watson and Hillman 1997, Vadas and Orth 2000).

The scale of an investigation of distribution addresses both study extent and grain (Weins 1989). For the purposes of this investigation, I adjust scale by altering the individual unit of observation, or grain size, but do not alter the overall area under

investigation (extent). I test two alternative hypotheses to propose tentative “rules” that may be followed in similar multi-scale habitat studies to improve the likelihood of successful model transfer. I first hypothesize that increasing the grain of habitat measurement will increase model transferability. Coarser scales of habitat measurement have been proposed to increase model transferability because a precise prediction of microhabitat use from one region or system to another is unlikely due to both subtle and obvious environmental differences among systems. Further, fishes may select larger areas with an array of suitable microhabitats rather than a single, transferable microhabitat type (Vadas and Orth 2000). Second, I hypothesize that models incorporating features at the grain for which habitat selection is the strongest will transfer more successfully than grains for which selection is weak. For example, if a species selects entire channel units (e.g. pools) rather than microhabitats of 0.1 m^3 , models describing habitat in terms of channel units should transfer more successfully than models based on, microhabitat descriptors. The strength of an aquatic species’ response to variation in environmental factors at multiple scales can identify which scale is most relevant for the target species and most appropriate for management goals (Bult et al. 1998).

OBJECTIVES

The purpose of this study is to identify key habitat features at meso- and micro-scales for two populations of a federally endangered darter endemic to Virginia, the Roanoke logperch (*Percina rex*). Current understanding of Roanoke logperch habitat use is based exclusively on data collected in the Roanoke River (Burkhead 1983 and Jenkins and Burkhead 1993). Adult logperch typically are found in deep, high velocity riffle and run habitats in clear, medium size, and medium gradient reaches. Roanoke logperch seem intolerant of moderately to heavily silted substrates, possibly due to the feeding behavior unique to the subgenus *Percina*. Logperch use their conical snout to flip gravel and feed on exposed invertebrates. This exploits prey sheltered beneath rocks that may be unavailable to other benthic fishes; however, this feeding behavior relies on the availability of loosely embedded substrate. Habitat use by logperch outside of the

Roanoke River is largely unknown, including the population in the Nottoway River (Rosenberger and Angermeier 2002). Differences in habitat availability between these rivers may influence patterns of habitat use.

I define microhabitat as characteristics of the habitat immediately surrounding observed fishes (1 m²), and mesohabitat as characteristics of pools, riffles, and runs, i.e. commonly-used habitat strata at the reach scale (Frissel et al. 1986, Vadas and Orth 1998). My objectives in this study are to: 1) describe differences between the Roanoke and Nottoway rivers in available micro- and meso-habitat; 2) compare habitat use patterns of Roanoke logperch in both rivers at micro- and meso-habitat scales; and 3) examine transferability of habitat models at both scales. I relate differences between populations in micro- and meso-habitat use to differences in available habitat between rivers. These comparisons will be used to identify consistencies in habitat use patterns between rivers that are likely to reflect actual preferences of the species. Analyses also will indicate the strength of habitat selection at both scales and whether the models based on meso-habitat variables transfer more successfully than models based on micro-habitat variables.

Using univariate techniques, I examine differences among rivers in selection and use of individual habitat parameters. However, because logperch are likely responding to multiple habitat variables, multivariate techniques also are used. I use *G*-tests and Principal Components Analysis (PCA) to examine the strength of habitat selection at micro- and meso-habitat scales and to compare micro- and meso-habitat availability and use among rivers. I also use discriminant multivariate analysis to quantitatively examine multivariate differences among systems in habitat use and availability. Because discriminant analysis emphasizes separation among determined groups and identifies variables that differ the most among systems, it is used in this study to identify which variables account for significant differences among rivers in both available and used habitat configurations. I use logistic regression models set at micro- and meso-scales to examine habitat use patterns of logperch for each river. These models were transferred to among river systems, and transferability was evaluated in terms of the proportion of correct predictions.

METHODS

Study Sites

Within the Roanoke drainage, isolated populations of logperch occur in the upper Roanoke, Pigg, and Smith rivers. Within the Chowan drainage, logperch are distributed along the fall zone between the piedmont and coastal plain physiographic provinces in the Nottoway River. The greatest population densities of Roanoke logperch are in the upper Roanoke River (Burkhead 1983, Jenkins and Burkhead 1993) and in the Nottoway River drainage (Rosenberger and Angermeier 2002). For the purposes of this study, I concentrated on these two populations (Figure 2.1). The Roanoke River is a clear, coolwater, high gradient system that empties into the Albemarle Sound. Cattle farming and construction along the stream banks contribute silt loads to the river and its tributaries. The Nottoway River is located in eastern Virginia and empties into the Atlantic Ocean via the Chowan drainage. This river is tannin-stained, warmwater, and lowland (Jenkins and Burkhead 1993). The Nottoway River is similar in gradient to the Roanoke River only in the Fall Zone between the Piedmont and Coastal Plain physiographic provinces, where riffle and run habitat similar to the montane rivers occur. The Nottoway River fauna is closely related to the fauna of the Roanoke River due to historic connection between the Roanoke and Chowan rivers; however, the Nottoway River contains additional species characteristic of the coastal plain and lower piedmont. The Nottoway River has an intact riparian zone that presumably prevents heavy sedimentation in the stream resulting from human activity in its watershed.

Mesohabitat sampling

Habitat inventories were completed for 10 contiguous river kilometers of the Roanoke River and 20 kilometers of the Nottoway River. These lengths allowed the sampling of a wide range of habitat types. Along each length of river, habitat inventory was conducted via the basinwide visual estimation technique (BVET, Hankin and Reeves 1988; Dolloff et al. 1993). A two- to three-person crew classified and inventoried habitat strata along each reach of river. High gradient areas with convex stream bottoms, turbulent water surfaces, and fast water were classified as riffle habitat, and deep, low

gradient, slow moving areas with concave stream bottoms were classified as pools. Runs were defined as intermediate gradient areas with flat stream bottoms, fast water, and smooth water surfaces (Beschta and Platts 1986, Frissel et al. 1986, Hawkins et al. 1993, Vadas and Orth 1998). One crew member identified each habitat unit by type (pool, run, or riffle), recorded data, and took channel width measurements along the stream with an optical range finder. The second crew member visually classified the dominant and subdominant substrate by particle size (using a 9 – category Wentworth scale), average silt cover (5 categories: 1 = 76-100% cover, 2 = 51-75%, 3 =26-50%, 4 = 1-25%, 5 = 0%), and embeddedness of larger substrates (i.e. boulders, cobble, and gravel; 5 categories: 1 ≥ 95% embedded, 2 = 50-94%, 3 = 25-49%, 4 = 1-24%, 5 = 0%, i.e. exposed) in smaller substrates (i.e. silt and sand). This crewmember also estimated the minimum, maximum, and average depth of each habitat unit by measuring these parameters at multiple points along the habitat unit while traveling downstream and across the channel in a zigzag pattern. The final crew member measured the length of each habitat unit and the presence and abundance of woody debris. Woody debris >50cm diameter or >5m long was counted and assigned to classes measured along a four-category scale following Flebbe (1999; 1: >50 cm diameter, 1-5 m length; 2: 10-50 cm diameter, >5 m length; 3: >50 cm diameter, > 5 m length; and 4: root wads).

Stratified, systematic sampling of habitat increases the probability of detecting discontinuities in a species' distribution (Angermeier et al. 2002); therefore, I sampled sites that contained a pool, run, and riffle. For both rivers, eight riffle-run-pool series were systematically selected from the reach-wide inventories for summer quantitative underwater observation (Figure 2.1). Each habitat unit (pool, riffle, or run) was surveyed for logperch using line-transect snorkeling methods (see next section) and the following information was recorded for each unit: unit type (rank 1 = pool, 2 = run, 3 = riffle); closest distance to like habitat unit (m); unit width (m), length (m), and estimated area (m²); maximum and average depth (cm); dominant and subdominant substrate (rank categories); and substrate embeddedness and silt cover (rank categories).

Microhabitat sampling

Summer survey observations for each riffle-run-pool series were made via line-transect snorkeling methods described in Ensign et al. (1995). One to three parallel lines oriented with river flow were marked with yellow line on the day of sampling. Spacing between lines was a minimum of 1.5 times maximum underwater visibility on the day of sampling. The length of the lines was based on the length of the habitat units but did not exceed 50m per unit (150m per site). Visibility was determined by suspending a Secchi disk in the water column in front of a snorkeler. The snorkeler moved away from the disk until the black patterns on the disk were no longer distinguishable from the water. The distance between the snorkeler and the disk was measured and served as the maximum visibility for that day. Surveys were not conducted if maximum visibility was less than 1.5 meters (Leftwich et al. 1997).

To minimize effects of disturbance and to allow fish to settle, snorkelers did not begin sampling until at least one hour after placement of the transect lines. Snorkelers entered the water downstream of the area to be sampled and moved slowly upstream along the lines, keeping the center of the body over the line. Each observer scanned the stream bottom, mid-water, and upper-water column directly in front and to both sides of the line of travel. When an adult Roanoke logperch was sighted, a numbered weighted marker was placed on the stream bottom precisely where the fish was first spotted. The number-code of markers were recorded on dive slates. Double counting of logperch was avoided by simultaneously sampling all three transect lines with snorkelers staying even with each other while moving upstream. Continuous communication between snorkelers also minimized double counting. After the riffle-run-pool sequence was sampled, snorkelers returned to the base of the transects to count markers and collect habitat data.

Microhabitat data included water depth, bottom and mean water velocities, and point substrate size (nine-category Wentworth scale). Substrate characteristics within a 1-m² area around the marker also were recorded, including dominant and subdominant substrate size, embeddedness (5 categories: 1 = $\geq 95\%$ embedded, 2 = 50-94%, 3 = 25-49%, 4 = 5-24%, 5 = 0-5%, i.e. exposed), and silt cover (5 categories: 1 = 76-100% of area blanketed with deposited silt, 2 = 51-75%, 3 = 26-50%, 4 = 1-25%, 5 = 0%). To record microhabitat availability, I placed horizontal transects along the wetted width of

the river at 10-meter intervals along the length of the site within 24 hours of the snorkeling run. Every three meters on the horizontal transects, depth, mean and bottom water velocities and silt cover were recorded. I also recorded dominant and subdominant substrates, silt cover, and embeddedness within a 1-m² area for each of the availability locations.

Data Analysis

All data analyses, with the exception of the logistic regression models, were performed using SYSTAT (Version 9, Copyright © SPSS Inc., 1998). I used t-tests to compare meso- and micro-habitat availability between the Roanoke and Nottoway rivers. Mesohabitat availability was described by unit width, length, and area; average and maximum depth; average number of woody debris pieces of sizes 1 through 4; average dominant and subdominant substrate, and average substrate embeddedness and silt cover. Microhabitat availability was described by depth, bottom and mean velocity, dominant and subdominant substrate, embeddedness, and silt cover. All variables were separated by mesohabitat type (pool, run, or riffle) before analysis.

G-tests with Williams' correction (Williams 1976) were used to detect meso- and microhabitat selection by logperch for each river by comparisons of actual habitat use with that expected if logperch used habitat randomly. Additional mesohabitat variables used for this analysis included unit type (1 = pool, 2 = run, 3 = riffle) and distance to like habitat (m). Woody debris categories were collapsed into a single mesohabitat variable, the total amount of woody debris. Differences in logperch habitat use between the two rivers for individual habitat characteristics were tested with Mann-Whitney *U* tests for mesohabitat variables and ranked microhabitat variables and *t*-tests for continuous microhabitat variables. Non-parametric tests were used for small sample sizes and because ranked data did not meet normality assumptions. Multivariate analysis of logperch micro- and mesohabitat use in comparison to available habitat in all three rivers was examined with principal components analysis (PCA) using a correlation matrix with varimax rotation. Linearity assumptions were verified for each PCA. In addition, PCA was used to show patterns of differences between rivers in habitat use by Roanoke logperch. Differences between rivers in logperch habitat use were additionally examined

with multivariate analysis of variance (MANOVA), and discriminant analysis including a jackknifed classification matrix and canonical discriminant functions.

I developed two separate logistic regression models, one relating microhabitat variables to logperch presence and the other relating mesohabitat variables to logperch presence (SAS® System Version 8.2, Cary, NC; Allison 1999). In order to obtain the most parsimonious models possible, variables used in the logistic regression, including interaction terms, were eliminated from models in a stepwise fashion if they strongly covaried with other habitat variables or did not significantly contribute to the fit of the model (no or slight increase in AIC criterion or a non-significant Wald Chi-square). Multicollinearity assumptions were met for each model. For mesohabitat models, unit type (pool, riffle, or run) was considered a class variable.

I verified the fit of these models by evaluating the ability of the model to predict the presence of logperch (sensitivity) versus available habitat (specificity) in the data set from which the model was developed. Sensitivity measures the ability of the model to correctly identify presences (sensitivity = “# of true presences” / [“# of true presences” + “# of false absences”]). Specificity measures the ability of the model to correctly identify absences (specificity = “# of true absences” / [“# of true absences” + “# of false presences”]). Logistic regression assumes that absences in the data set are true absences, while, in this case, absences are habitat availability data points and “presences” are nested within available habitat. Following model self-verification, I then examined whether microhabitat and mesohabitat models developed in one river were applicable to microhabitat and mesohabitat data sets from the other river (transferability). Each model was evaluated for its sensitivity and specificity to assess transferability. Success of transfer was evaluated against values obtained for model self-verification. I did not use % correct overall to evaluate model transferability or to verify models because the data set was highly biased towards availability data points.

For the analysis, a 0.50 “cutoff” probability level for predicting the presence of logperch was not appropriate for purposes of model verification and transferability for two reasons: 1) the data do not consist of presences and absences, but rather presences and availability, and 2) the data set overwhelmingly comprises availability data points, which drive the outcome. I therefore used a cutoff value equal to the number of

presences in the data set divided by the number of availability data points (availability bias; Hosmer and Lemeshow 1989). When I verified the models using a variety of cutoff levels (0.01 to 1 at 0.01 intervals), I found that the cutoff probabilities derived from the availability bias closely approximated the probabilities that maximized model sensitivity and specificity (Hosmer and Lemeshow 1989). For the purposes of model verification, I used a cutoff value that equaled the availability bias for the river for which the model was developed (for microhabitat models: Roanoke River = 0.07, Nottoway River = 0.03; for mesohabitat models: Roanoke River = 0.07; Nottoway River = 0.10). To examine transferability, I used a cutoff value equal to the availability bias for the combined data sets (both rivers combined: microhabitat = 0.047; mesohabitat = 0.08).

RESULTS

Habitat availability

Summarized BVET data indicated that pool habitat is dominant, runs uncommon, and riffles rare in the Nottoway River relative to the Roanoke River (Table 2.1). This is expected due to difference in gradient between the two rivers. Pools in the Nottoway River contain more medium woody debris (rank 2: 10-50 cm diameter, >5 m length; $t = 39.8$, $P < 0.001$) and large woody debris (rank 3: >50 cm diameter, > 5 m length; $t = 6.1$, $P = 0.01$) than pools in the Roanoke River. Although Nottoway River pools have smaller dominant substrates (i.e., sand) than pools in the Roanoke River ($t = 17.2$, $P < 0.001$), and larger substrates such as gravel, cobble, and debris in Nottoway River pools were dramatically less embedded and silt-free in comparison to larger substrates in Roanoke River pools ($t \geq 27.8$, $P < 0.001$). Medium-sized woody debris is more frequently encountered in Nottoway River runs ($t = 16.9$, $P < 0.001$), which are deeper, less silted, and less embedded than runs in the Roanoke River ($t \geq 6.3$, $P \leq 0.01$). Although silt cover in riffles does not differ significantly between rivers ($t = 0.65$, $P = 0.42$), substrate in Nottoway River riffles is less embedded ($t = 95.7$, $P < 0.001$). Roanoke River riffles are shallower than Nottoway River riffles ($t = 3.9$, $P = 0.05$). The predominance of bedrock in Nottoway River riffles results in a larger dominant substrate sizes than riffles in the Roanoke River ($t = 23.7$, $P < 0.001$). Root wads (#4 woody debris) are more

exposed in Roanoke River riffles ($t = 6.6$, $P = 0.01$), perhaps due to increased frequency of undercut banks. Medium-sized woody debris is more common in Nottoway River riffles than Roanoke River riffles ($t = 15.2$, $P < 0.001$).

Differences between rivers in habitat features, particularly substrate characteristics, showed similar trends when the grain size was decreased from mesohabitat to microhabitat. Microhabitat availability data indicated that sites surveyed for microhabitat use by Roanoke logperch in the Nottoway River are deeper than sites in the Roanoke River for all mesohabitat types ($t > 2.9$, $P \leq 0.004$, Table 2.1). Although microhabitat substrate sizes are smaller in the Nottoway River ($t = 4.4$, $P < 0.001$), microhabitat in Nottoway River pools, riffles, and runs was less embedded and covered with silt than microhabitat in the Roanoke River ($t \geq 4.4$, $P < 0.001$). Microhabitat velocities were higher for Roanoke River pools than Nottoway River pools ($t = 2.1$, $P = 0.03$), and bottom velocities were greater for Roanoke River riffles ($t = 3.1$, $P = 0.002$).

Univariate analysis of micro- and meso-habitat use by Roanoke logperch

Logperch in the Roanoke River were primarily observed in runs, occasionally in riffles, and rarely in pools (Table 2.2). Differences in Roanoke logperch mesohabitat use in the Nottoway River are striking; logperch were observed primarily in pools, occasionally in runs, and rarely in riffles. Mesohabitats in the Nottoway River containing logperch had a lower unit rank, reflecting logperch use of lower velocity habitats in this river ($\chi^2 = 8.5$, $P = 0.004$). Mesohabitat units with logperch in the Nottoway River were also larger and deeper than units with logperch in the Roanoke River ($\chi^2 \geq 5.5$, $P \leq 0.02$). Roanoke River habitat units with logperch had larger substrate sizes than mesohabitats with logperch in the Nottoway River ($\chi^2 \geq 5.7$, $P \leq 0.02$), while Nottoway River mesohabitats with logperch contained more woody debris ($\chi^2 = 10.7$, $P = 0.001$). Logperch in the Roanoke River did not appear to select for particular mesohabitat characteristics, except selection for units with boulders as their subdominant substrate ($G = 12.5$, $P = 0.004$) and marginal selection for faster water habitat units ($G = 4.6$, $P = 0.10$) with less woody debris ($G = 7.2$, $P = 0.03$). I also observed little selection for mesohabitat characteristics in the Nottoway River; marginal selection was observed for

slower water habitat units ($G = 5.7, P = 0.06$) with moderately embedded substrates ($G = 8.5, P = 0.08$).

Logperch observed in the Roanoke River selected deep, high velocity microhabitats with exposed, silt free gravel substrate ($G \geq 23.7, P < 0.001$) and did not appear to select for bottom velocities ($G = 1.3, P = 0.83$, Table 2.3). In contrast, Roanoke logperch in the Nottoway River selected deep microhabitats with medium mean velocities and low bottom velocities ($G \geq 11.3, P \leq 0.01$). Logperch in the Nottoway River did not appear to select for substrate or embeddedness categories ($G \leq 10.6, P \geq 0.02$), but selected substrates free of silt ($G = 16.9, P = 0.005$).

Although logperch consistently selected relatively deep habitats, there were significant differences between rivers. Nottoway River logperch selected the deepest habitat ($t = 6.1, P < 0.001$, Table 2.4). I also observed variation in the use of water velocities. Roanoke River logperch were found in water with faster mean and bottom velocities than logperch in the Nottoway River (i.e. pools; $t \geq 2.6, P \leq 0.02$). However, Roanoke logperch in the Roanoke and Nottoway rivers were remarkably consistent in their use of substrate characteristics. Logperch were observed consistently over small to large gravel (ranks 5 and 6, $t = 0.5, P = 0.48$) in areas dominated by large gravel to boulders (ranks 6 through 8, $t = 2.4, P = 0.12$). Subdominant substrates around the points where the logperch were observed in both rivers consisted of small to large gravel (ranks 5 and 6, $t = 1.6, P = 0.21$). Although there were differences between rivers in embeddedness and silt characteristics and logperch use of pools, riffles, and runs, I did not detect a significant difference among rivers in the embeddedness and silt cover of substrates over which logperch were observed ($t \leq 3.3, P \geq 0.07$). Roanoke logperch were consistently observed over loosely embedded substrate with little to no silt cover.

Multivariate analysis of micro- and meso-habitat use by Roanoke logperch

PCA showed that mesohabitat units varied considerably in physical features. Mesohabitat unit type, area, depth, silt cover, and woody debris loaded the first component most heavily, while shortest distance to like habitat, unit type, and silt cover heavily loaded the second component (Table 2.5). These rotated axes explain 28.5 and 15.1% of the variance in the data, respectively. When PCA scores for availability and

habitat use locations are plotted in two-dimensional multivariate space (Figure 2.2), the first axis represents small, higher gradient, erosional mesohabitats with little woody debris versus large, low gradient, depositional mesohabitats with woody debris. The second axis represents widely spaced, high gradient mesohabitats with less silted substrates versus closely spaced, low gradient mesohabitats with silt. Polygons circumscribe the area occupied by habitat availability data points for the two rivers.

Roanoke River mesohabitat covers less multivariate space and is a subset of Nottoway River mesohabitat data for both habitat availability and habitat use. PCA indicates a wider availability of mesohabitat characteristics in the Nottoway River, particularly large, low gradient mesohabitats with an abundance of woody debris (Figure 2.2). Units that contain logperch are widely spread along the first axis for both rivers and tend to cluster towards the bottom of the second axis, representing faster habitats with less silt. Mesohabitats where logperch were observed occupied a range of configurations along each axis and overlap significantly between rivers. Relative frequency of availability data points indicates that mesohabitat configurations used by Roanoke logperch are not rare in either system. This is consistent with univariate analyses indicating lack of strong selection of mesohabitat characteristics.

PCA indicates extensive overlap in microhabitat availability between rivers (Figure 2.3). Logperch use a range of microhabitat configurations in each river, but are not found in extremes along axes or areas with the slowest velocities and the most silted and embedded substrates. Logperch locations from the two rivers along both axes overlap significantly. Logperch locations along Axis 1 indicate that logperch in the Roanoke River range from the slowest to the fastest water, whereas Nottoway River logperch occupy only slow to intermediate velocities. This corroborates univariate analysis, which indicates that logperch in the Roanoke River can be found in the fastest waters available (Table 2.4). Relative frequency of availability data points indicates that logperch in the Nottoway River occupy microhabitats that are readily available; while logperch in the Roanoke River occupy both common and rare microhabitats.

Multivariate mesohabitat use by adult Roanoke logperch differed significantly between the Roanoke and Nottoway rivers ($F = 11.1$, Wilk's lambda = 0.11, $P < 0.001$). The analysis correctly classified 89% of the mesohabitats containing logperch to the river

from which the data were collected (Table 2.6). Canonical discriminant functions indicate that the variables “shortest distance to like mesohabitat” and “total woody debris” were the two mesohabitat variables most useful for separating logperch presence between the two rivers. This is probably due to differences between rivers in available habitat rather than actual logperch mesohabitat preference. The Nottoway River has considerably more woody debris and is a larger system, with larger units that are spread more widely (Table 2.2).

Multivariate microhabitat use by logperch also significantly differed between the Roanoke and Nottoway rivers ($F = 16.5$, Wilk’s lambda = 0.38, $P < 0.001$). This analysis correctly classified data to its river 86% of the time, a similar frequency to the mesohabitat classification (89%, Table 2.6 and 2.7). Again, the analysis corroborated univariate analysis by indicating differences between rivers in logperch use of depth (Table 2.7). However, unlike univariate analysis, canonical discriminant functions also indicated that silt cover was an important variable differentiating logperch habitat use between the two systems. This difference in use of habitat variables may be a result of differences between systems in available habitat. Deeper, less silted habitats were more common in the Nottoway River than in the Roanoke River (Table 2.1).

Logistic regression analysis

All of the logistic regression models showed a non-uniform distribution of Roanoke logperch in the Roanoke and Nottoway rivers (Chi-square ≥ 15.5 , $P \leq 0.001$, Table 2.8). The mesohabitat logistic regression model for the Roanoke River indicates that logperch are negatively associated with pools and riffles and prefer larger, silt free substrates. In addition, logperch appeared to be negatively associated with woody debris in Roanoke River. This does not corroborate univariate analyses (G -tests) that indicate weak or no selection for these mesohabitat characteristics. The mesohabitat model developed from the Nottoway River indicates that logperch are positively associated with mesohabitats that are close to like habitats and contain large subdominant substrates. Again, I did not detect this selection with univariate analyses (Table 2.3).

In contrast, patterns of microhabitat use indicated by logistic models are consistent with univariate analyses. The model for the Roanoke River indicated that

logperch prefer deep, fast-moving waters with large substrates and low silt cover. Further, it indicates that logperch choice of substrate sizes and silt cover was dependent on the velocity of these habitats. This logistic equation, when applied to my original Roanoke River data set, correctly predicted presences far better (93%) than availability (43%, Table 2.9). Although the Roanoke River mesohabitat model was not as accurate as the microhabitat model in predicting logperch presence (75% vs. 93%), the mesohabitat model had greater specificity (88%). The microhabitat model developed for the Nottoway River indicated that logperch prefer deep, slower moving water with low silt cover and larger dominant substrates in this system (Table 2.8). This model correctly predicted only 56.7% of logperch presences but 83.7% of the availability data points (Table 2.9). The mesohabitat model predicted the presence of logperch more accurately (73%) than the microhabitat model. However, the microhabitat model had greater specificity than the mesohabitat model (84% vs. 65%).

Model transfer

Transferred microhabitat models had greater sensitivity values than mesohabitat models. The microhabitat models developed in the Roanoke River correctly classified 97% of logperch presences in the Nottoway River data set, while the mesohabitat model did not predict the presence of any logperch in the Nottoway River (Table 2.9). Both the microhabitat and mesohabitat models developed for the Nottoway River performed poorly when applied to the Roanoke River data set to predict logperch presence (microhabitat = 2%, mesohabitat = 0%). However, the sensitivity of the Roanoke River mesohabitat model was greater when applied to the Nottoway River data set (88%) than the microhabitat model (29%). The Nottoway River models, when transferred, showed an opposite trend. The mesohabitat model did not predict habitat availability (61%) in the Roanoke River as well as the microhabitat model.

DISCUSSION

Habitat availability and logperch habitat use in the Roanoke and Nottoway rivers

Significant separation among many habitat characteristics between the Roanoke and Nottoway rivers are probably due to differences between the rivers in physiography, gradient, and anthropogenic disturbance. The most consistent and dramatic differences in mesohabitat characteristics are in embeddedness, silt cover, and frequency of woody debris. The Nottoway River is relatively pristine and undeveloped compared to the Roanoke River. Intact riparian zones in the Nottoway River contribute woody debris and stabilize banks, which, in turn, reduce sediment loads that cover and embed substrate. Exposed root wads, more common in Roanoke River riffles than Nottoway River riffles, are sometimes the result of undercutting that characterizes an unstable channel streambank. The Nottoway River is a larger and wider system than the upper Roanoke, thus the presence of deeper runs and riffles in the Nottoway River. Microhabitats are much less silted and embedded in the Nottoway River. The Roanoke River provides faster microhabitat with larger substrates than the Nottoway River. Despite these differences, PCA indicated overlap between the two systems in both meso- and micro-habitat characteristics, indicating that habitat use patterns could transfer successfully between the two systems.

I did not observe clear selection for mesohabitat characteristics in either river; further, little consistency was apparent between systems in mesohabitat use. Among the most striking differences between the two systems was in the differential use of pools, runs, and riffles. Logperch in the Nottoway River appear to use slower velocity mesohabitats than logperch in the Roanoke River. Despite these differences, Roanoke logperch were surprisingly consistent in their use of microhabitat substrate characteristics. Logperch in both rivers were found over silt-free, loosely embedded gravel substrate. Although most descriptions of logperch microhabitat use thus far have been based on depth and velocity preferences (Burkhead 1983, Jenkins and Burkhead 1993), logperch are not consistent in their use of velocity and depth characteristics between populations.

Habitat use patterns and life-history characteristics of Roanoke logperch

Consistency in the use of substrate characteristics indicates that microhabitats with suitable substrate are the most likely distributional limiting factor for logperch, and

adult logperch will occupy a variety of depths, velocities, and mesohabitat types to accommodate substrate requirements. This may be due to the unique feeding strategy of logperch. By flipping small rocks and debris to feed on exposed insects, logperch rely on the availability of small, loosely embedded substrate. Habitat availability data indicate that fast velocity habitat similar to what logperch use in the Roanoke River is available in the Nottoway River. Low silt loads and woody debris in Nottoway River pools may enable logperch to thrive in these habitats. Mean values of silt and embeddedness characteristics of Nottoway River pools correspond closely with mean microhabitat use values of silt and embeddedness for logperch in all river systems. Silt cover and embeddedness characteristics of Roanoke River pools fall far below conditions preferred by Roanoke logperch. Further, woody debris common in the Nottoway River can provide shelter from predators and can serve as substrate for invertebrates and provide food for foraging fishes (Angermeier 1985). Use of low velocity habitats such as pools in the Roanoke River may not be an option for Roanoke logperch because of excessive silt loads and reduced woody debris. Fausch (1983) demonstrated that habitat selection by salmonid fishes maximized foraging profitability, which was a function of food availability and swimming cost. Logperch in the Roanoke River may not be able to forage successfully in slow velocity habitats; therefore, they may be experiencing a higher energetic cost than Nottoway River logperch to forage in fast water habitats. Plasticity in selection of depth and velocity characteristics may account for logperch persistence in the Roanoke River under suboptimal conditions.

Model transferability and spatial scale of investigation

Increasing the scale of measurement from microhabitat to mesohabitat did not appear to improve accuracy of logistic regression models. Logistic models based on mesohabitat characteristics were poor predictors of logperch presences in the two systems. The limited success of mesohabitat logistic models can be entirely attributed to their specificity. The lack of strong mesohabitat selection in either system indicates that this scale of measurement is not useful if we wish to transfer our knowledge of logperch habitat use between systems. Consistency in use of and strong selection for microhabitat

substrate characteristics may account for the increased sensitivity of microhabitat models when transferred between systems.

The data sets used for logistic regression were heavily biased towards habitat availability, which may have contributed to weak model transfer. Logistic regression treated availability data points as “absences,” while, in actuality, “presences” are nested within available habitat. This weakens the conclusiveness of the models. This is not an uncommon problem with ecological data. Typically, “absence” data is less reliable than “presence”. Models that incorporate this uncertainty may transfer better among systems (Bayley and Peterson 2001). Further, each model reflects habitat availability of the river system in which it is developed. Its predictive power is weakened in systems with available habitat configurations that range outside the data set on which the original model was based, particularly if Roanoke logperch occupy a variety of depths, velocities, and mesohabitat types. This argues for the development of composite models based on data from multiple systems that incorporate a larger range of features for model transfer. For both meso- and micro-habitat use, PCA appeared to perform better in predicting suitable locations for Roanoke logperch and may prove a better tool than logistic regression for examining the suitability of habitat configurations for a target species in an unsampled river. Leftwich et al. (1997) also found PCA more useful than logistic regression in predicting optimal habitat among systems. Regardless of the analysis, logperch microhabitat use patterns appear to be more transferable between systems than logperch mesohabitat use patterns.

Implications

Pinpointing invariant distributional patterns, consistently used habitat configurations, and strength of selection over multiple scales gives insight regarding what scale is most relevant for management. Clear selection for microhabitat characteristics and consistency in microhabitat substrate preferences between systems indicates that the micro-scale is more relevant for the management of Roanoke logperch than the meso-scale. However, the use of mesohabitat types and examination of mesohabitat preferences between rivers offered insight to the biological significance of logperch microhabitat preferences, indicated potential stressors for the species at larger scales (i.e.,

heavy silt loads), and suggested paucity of preferred habitat in the Roanoke River (i.e., pools with woody debris). Management to enhance populations of Roanoke logperch should focus on the enhancement of riparian zones and protect streambanks from agricultural and construction practices that contribute sediment. This type of management is ongoing in the upper Roanoke River; however, efforts will need to be more widespread to enhance slow-water habitats in the Roanoke River. These practices need to be applied at the watershed scale to achieve micro-scale results. Complete riparian zones will also contribute woody debris to low velocity mesohabitats. Scouring flow during flood events should also enhance microhabitat through removal of small sediments.

This study suggests that increasing scale of measurement does not necessarily improve the transfer of habitat models. However, this trend may hold only for species with life history characteristics similar to the Roanoke logperch. Species that vary in life history characteristics may differ at the scale at which they show habitat selectivity (e.g., shortnose and Atlantic sturgeon, Kynard et al. 2000). Hydraulic variables and turbulence are the best discriminators of mesohabitat types (e.g. pool, run, riffle); while substrate and roughness variables are less useful (Vadas and Orth 1998). Species like the Roanoke logperch that are sensitive to substrate characteristics at the micro- scale may be less likely to respond to variation at the habitat unit scale because substrate characteristics do not reliably stratify between pools, riffles, and runs. Other methods for increasing scale besides using riffle, run, pool units may be more effective for describing the habitat use of substrate specialists. Systematically increasing the grain of habitat characterization (1-m² to 10-m² to 100-m² and so on), without regard to pool-riffle morphology would allow a fairer test of the effect of scale on model transferability.

For the purposes of model transferability, it is clear that the scale at which data are collected should not be chosen arbitrarily. Models that incorporate factors that are directly related to the fitness of the species are more likely to transfer between localities because these needs will be consistent regardless of environmental context. This study suggests that examining the selectivity of habitat characteristics at different scales can give significant insight to what variables are more likely to be directly related to the fitness of the study species and therefore more likely to be useful for transferring a

model. Examination of both life history characteristics and the strength of habitat selection when choosing variables for a transferable model should improve habitat studies of this kind. Future studies should examine transferability of habitat models for species that vary in life history characteristics and the scale of measurement for which they show strong selection of habitat features.

It should be noted that this study is limited to the use of habitat by only a single life stage. YOY logperch use backwater and secondary channel habitats that are not incorporated into this study. Therefore, larger-scale models that incorporate these channel characteristics may be necessary for the management of multiple life stages. Finally, the two scales chosen for this study are relatively small; future studies should examine if a reach- or basin-wide approach suggest larger patterns that lend additional insight for model transfer.

Table 2.1 Summary of mesohabitat (A) and microhabitat (B) characteristics (mean \pm standard deviation) of pools, riffles, and runs in the Roanoke and Nottoway rivers. *Indicates a significant difference between rivers at the 0.05 level (*t*-tests).

(A)				
POOL CHARACTERISTICS	Roanoke River	Nottoway River	<i>t</i>	<i>P</i>
Width (m)	24.5 \pm 9.3	32.2 \pm 9.5	5.7	<0.001 *
Length (m)	90.8 \pm 81.5	216.4 \pm 272.7	3.7	<0.001 *
Area (m ²)	2333 \pm 2378	7438 \pm 100032	4.2	<0.001 *
Depth (cm)	79.3 \pm 47.6	76.1 \pm 33.3	0.4	0.53
Maximum depth (cm)	113.3 \pm 69.9	109.6 \pm 50.1	0.23	0.63
# 1 woody debris/unit	0.1 \pm 0.2	0.0 \pm 0.3	0.47	0.49
# 2 woody debris/unit	2.0 \pm 3.9	7.7 \pm 8.5	39.8	<0.001 *
# 3 woody debris/unit	0.5 \pm 1.2	1.0 \pm 1.7	6.1	0.01 *
# 4 woody debris/unit	3.5 \pm 5.3	3.4 \pm 5.0	0.01	0.91
Rank dominant substrate	6.8 \pm 1.9	5.7 \pm 2.2	17.2	<0.001 *
Rank subdominant substrate	5.8 \pm 2.0	6.0 \pm 2.7	0.28	0.6
Rank embeddedness	1.7 \pm 0.7	4.2 \pm 0.7	680.4	<0.001 *
Rank silt cover	2.6 \pm 1.5	3.5 \pm 1.2	27.8	<0.001 *
<i>N</i>	69	64		
RUN CHARACTERISTICS				
Width (m)	26.7 \pm 9.4	31.6 \pm 11.3	3.0	0.03 *
Length (m)	42.4 \pm 55.6	74.4 \pm 62.1	2.6	0.003 *
Area (m ²)	1233 \pm 2645	2285 \pm 1869	2.2	0.01 *
Depth (cm)	32.1 \pm 11.0	41.3 \pm 17.6	11.5	<0.001 *
Maximum depth (cm)	48.0 \pm 18.2	62.5 \pm 24.5	13.9	<0.001 *
# 1 woody debris/unit	0.0 \pm 0.2	0.0 \pm 0.1	0.7	0.4
# 2 woody debris/unit	0.9 \pm 1.6	3.0 \pm 3.7	16.9	<0.001 *
# 3 woody debris/unit	0.2 \pm 0.5	0.3 \pm 0.9	2.1	0.15
# 4 woody debris/unit	1.6 \pm 2.0	1.5 \pm 2.5	0.16	0.67
Rank dominant substrate	6.8 \pm 1.4	6.2 \pm 2.4	3.2	0.08
Rank subdominant substrate	6.3 \pm 1.5	6.3 \pm 2.4	0	0.97
Rank embeddedness	2.1 \pm 0.7	3.1 \pm 1.2	23.4	<0.001 *
Rank silt cover	3.8 \pm 1.3	4.3 \pm 0.19	6.3	0.01 *
<i>N</i>	39	44		
RIFFLE CHARACTERISTICS				
Width (m)	21.7 \pm 9.8	32.6 \pm 15.7	3.6	0.42
Length (m)	31.8 \pm 21.7	27.3 \pm 23.9	0.9	0.001 *
Area (m ²)	714 \pm 647	873 \pm 956	0.8	0.39
Depth (cm)	22.3 \pm 11.7	27.2 \pm 19.0	3.9	0.05 *
Maximum depth (cm)	36.1 \pm 22.0	41.9 \pm 21.5	2.8	0.1
# 1 woody debris/unit	0.0 \pm 0.2	0.0 \pm 0.0	2.3	0.13
# 2 woody debris/unit	0.7 \pm 1.3	1.9 \pm 2.3	15.2	<0.001 *
# 3 woody debris/unit	0.1 \pm 0.3	0.4 \pm 1.4	3.4	0.07
# 4 woody debris/unit	1.2 \pm 1.3	0.6 \pm 1.6	6.6	0.01 *
Rank dominant substrate	7.1 \pm 1.0	8.1 \pm 1.4	23.7	<0.001 *
Rank subdominant substrate	6.5 \pm 1.2	6.4 \pm 1.8	0.15	0.7
Rank embeddedness	2.8 \pm 0.8	4.3 \pm 1.0	95.7	<0.001 *
Rank silt cover	4.7 \pm 0.8	4.8 \pm 0.7	0.65	0.42
<i>N</i>	54	28		

Table 2.1 (cont)

(B)

POOL CHARACTERISTICS	Roanoke River	Nottoway River	<i>t</i>	<i>P</i>
Depth (m)	75.7 ± 45.1	84.9 ± 35.9	2.9	0.004 *
Bottom velocity (m/s)	0.06 ± 0.24	0.04 ± 0.09	1.9	0.06
Mean velocity (m/s)	0.21 ± 0.45	0.15 ± 0.15	2.1	0.03 *
Rank dominant substrate	5.9 ± 2.5	4.7 ± 2.2	6.2	<0.001 *
Rank subdominant substrate	4.8 ± 1.9	4.6 ± 2.4	1.1	0.28
Rank embeddedness	2.5 ± 1.4	3.5 ± 1.3	9.5	<0.001 *
Rank silt cover	2.4 ± 1.5	3.4 ± 1.5	8.4	<0.001 *
<i>N</i>	270	401		
RUN CHARACTERISTICS				
Depth (m)	35.8 ± 21.16	50.7 ± 24.0	7.5	<0.001 *
Bottom velocity (m/s)	0.08 ± 0.16	0.07 ± 0.13	0.73	0.46
Mean velocity (m/s)	0.25 ± 0.31	0.28 ± 0.33	1.2	0.23
Rank dominant substrate	7.0 ± 1.7	5.4 ± 2.2	9.1	<0.001 *
Rank subdominant substrate	5.9 ± 1.6	5.1 ± 2.1	5.0	<0.001 *
Rank embeddedness	3.3 ± 1.3	3.9 ± 1.3	4.8	<0.001 *
Rank silt cover	3.4 ± 1.4	4.3 ± 1.2	7.3	<0.001 *
<i>N</i>	223	316		
RIFFLE CHARACTERISTICS				
Depth (m)	26.2 ± 16.3	34.3 ± 21.3	4.4	<0.001 *
Bottom velocity (m/s)	0.16 ± 0.30	0.08 ± 0.19	3.1	0.002 *
Mean velocity (m/s)	0.40 ± 0.44	0.37 ± 0.48	0.82	0.41
Rank dominant substrate	7.7 ± 1.0	6.9 ± 2.3	4.4	<0.001 *
Rank subdominant substrate	5.7 ± 1.6	5.6 ± 2.0	0.57	0.56
Rank embeddedness	3.7 ± 1.1	4.3 ± 1.1	5.0	<0.001 *
Rank silt cover	4.0 ± 1.4	4.5 ± 1.0	4.4	<0.001 *
<i>N</i>	202	220		

Table 2.2 Summary of mesohabitat characteristics of habitat units (pools, riffles, or runs) where adult Roanoke logperch were observed during snorkeling surveys in the Roanoke and Nottoway rivers, Virginia. *Indicates a significant difference at the 0.05 level (Mann-Whitney *U* tests).

	Roanoke River	Nottoway River	χ^2	<i>P</i>	
% Total logperch observed in	Pools	11%	69%		
	Riffles	22%	21%		
	Runs	67%	10%		
Unit type (mean rank, SD)	2.4 ± 0.7	1.5 ± 0.6	8.5	0.004	*
Distance to like habitat (m, SD)	119 ± 63	322 ± 334	6.7	0.1	
Width (m, SD)	26.6 ± 6.5	29.4 ± 9.5	0.61	0.43	
Length (m,SD)	42.4 ± 32.4	224 ± 372	4.5	0.03	*
Area (m², SD)	1085 ± 816	6360 ± 10136	5.5	0.02	*
Maximum Depth (cm, SD)	62.9 ± 19.4	104.7 ± 46.3	7.4	0.007	*
Average Depth (cm, SD)	39.6 ± 9.9	72.5 ± 35.4	8.6	0.003	*
Dominant Substrate (mean rank, SD)	8.2 ± 0.9	5.6 ± 2.4	6.4	0.01	*
Subdominant Substrate (mean rank, SD)	7.7 ± 1.1	5.2 ± 2.7	5.7	0.02	*
Embedddness (mean rank, SD)	2.9 ± 1.0	2.5 ± 1.1	0.88	0.35	
Silt Cover (mean rank, SD)	4.0 ± 1.3	3.7 ± 1.2	0.71	0.4	
Total Woody Debris (#, SD)	1.8 ± 2.0	27.4 ± 54.9	10.7	0.001	*
<i>N</i>	12	15			

Table 2.3 A summary of *G*-tests examining the frequency of logperch occurrences in meso- and micro-habitat categories relative to availability of those categories. A significant *G*-test indicates that logperch selected habitat categories disproportionately to their availability. The direction of this selection is presented for significant and marginally significant tests (NS = $P > 0.05$).

Mesohabitat Selection

	Roanoke River				Nottoway River			
	<i>G</i>	df	<i>P</i>	Direction of selection	<i>G</i>	df	<i>P</i>	Direction of selection
Unit type (rank)	4.6	2	0.10	riffles and runs	5.7	2	0.06	runs and pools
Distance to like mesohabitat (m)	5.7	3	NS		0.8	3	NS	
Unit Width (m)	2.6	3	NS		2	3	NS	
Unit Length (m)	2.1	3	NS		1.5	3	NS	
Unit Area (m ²)	0.7	3	NS		1.9	3	NS	
Maximum Depth (cm)	2.7	3	NS		2.4	3	NS	
Average Depth (cm)	2.9	3	NS		4.3	3	NS	
Dominant Substrate (rank)	3.9	3	NS		2.3	2	NS	
Subdominant Substrate (rank)	12.5	3	0.004	*	boulder substrate	1	2	NS
Embeddedness (rank)	2.5	3	NS		8.5	4	0.08	moderate embeddedness
Silt Cover (rank)	0.7	2	NS		4.2	2	NS	
Total Number Woody Debris	7.2	2	0.03		less woody debris	0.5	2	NS

Microhabitat Selection

Variable	Roanoke River				Nottoway River					
	<i>G</i>	df	<i>P</i>	Direction of selection	<i>G</i>	df	<i>P</i>	Direction of selection		
Depth (cm)	49.2	3	<0.001	*	deeper depths	69.9	5	<0.001	*	deeper depths
Mean Velocity (m/s)	52.9	4	<0.001	*	faster velocities	16.8	5	0.005	*	intermediate velocities
Bottom Velocity (m/s)	4.3	3	NS			11.3	3	0.01	*	slow bottom velocities
Dominant Substrate (rank)	44.5	3	<0.001	*	gravel substrate	10.6	3	0.02	*	gravel substrate
Subdominant Substrate (rank)	5.4	3	NS			14	4	0.007	*	gravel substrate
Embeddedness (rank)	23.7	4	<0.001	*	less embedded	6.8	4	NS		
Silt Cover (rank)	43.7	4	<0.001	*	less silted	16.9	4	<0.005	*	less silted

Table 2.4 A summary of microhabitat characteristics of point locations where adult Roanoke logperch were observed during snorkeling surveys in the Roanoke and Nottoway rivers, Virginia. *Indicates a significant difference at the 0.05 level (*t*-tests for continuous data, Mann-Whitney *U* tests for ranked data).

	Roanoke River	Nottoway River	<i>t</i>	<i>P</i>
Depth (cm), SD	51.5 ± 12.8	84.2 ± 27.8	6.1	<0.001 *
Mean Velocity (m/s), SD	0.59 ± 0.68	0.20 ± 0.17	3.9	<0.001 *
Bottom Velocity (m/s), SD	0.15 ± 0.30	0.02 ± 0.09	2.6	0.01 *
			χ^2	
Point Substrate (mean rank), SD	5.8 ± 1.6	5.1 ± 2.0	0.5	0.48
Dominant Substrate (mean rank), SD	7.2 ± 1.6	6.1 ± 2.1	2.4	0.12
Subdominant Substrate (mean rank), SD	5.4 ± 1.6	5.2 ± 2.2	1.6	0.21
Embeddedness (mean rank), SD	3.8 ± 1.1	4.2 ± 1.0	3.3	0.07
Silt (mean rank), SD	4.0 ± 1.2	4.5 ± 0.7	1.7	0.20
<i>N</i>	54	39		

Table 2.5 Loadings of habitat variables on the first two principal components and percent of total variance accounted for by each component for (A) mesohabitat use and availability data and (B) microhabitat use and availability data in the Roanoke and Nottoway Rivers, Virginia.

(B)

Principal
Components

	1	2
Eigenvalues	4.3	2.6
Habitat Variables		
Unit type	-0.62	0.51
Unit area	0.75	0.21
River width	0.29	0.09
Distance to like habitat	0.31	0.67
Average depth	0.69	-0.41
Maximum depth	0.35	-0.20
Embeddedness	-0.52	0.45
Silt cover	-0.63	0.50
Total woody debris	0.74	0.29
% Variance	28.5	15.1

(A)

Principal
Components

	1	2
Eigenvalues	2.7	1.1
Habitat Variables		
Depth	-0.12	-0.51
Bottom velocity	0.87	0.01
Mean velocity	0.86	0.14
Dominant substrate	0.05	0.67
Subdominant substrate	-0.04	0.59
Embeddedness	0.42	0.62
Silt cover	0.53	0.59
% Variance	38.0	15.9

Table 2.6 Jack-knifed classification matrix (A) and canonical discriminant functions (B) of a discriminant analysis examining differences between mesohabitats containing logperch in the Roanoke and Nottoway rivers, Virginia.

(A)

Canonical Discriminant Classification			
Data Source			
	Roanoke River	Nottoway River	Total
Roanoke River	10	2	12
Nottoway River	1	14	15
% Correct	83	93	

(B)

Variables	Canonical Discriminant Functions
Unit type	0.4
Shortest distance to like habitat	-2.8
Width	-0.5
Area	-0.4
Maximum depth	0.1
Average depth	-1.2
Dominant substrate	1.1
Subdominant substrate	1.2
Embeddedness	-0.5
Silt Cover	-0.3
Total woody debris	2.8

Table 2.7 Jack-knifed classification matrix (A) and canonical discriminant functions (B) of a discriminant analysis examining differences between the Roanoke and Nottoway rivers in logperch microhabitat use.

(A)

Canonical Discriminant Classification			
Data Source			
	Roanoke River	Nottoway River	Total
Roanoke River	50	4	54
Nottoway River	9	30	39
% Correct	93	77	

(B)

Variables	Canonical Discriminant Functions
Depth	0.9
Bottom velocity	-0.1
Mean velocity	-0.5
Point substrate	0.06
Dominant substrate	-0.3
Subdominant substrate	-0.3
Embeddedness	-0.1
Silt Cover	0.9

Table 2.8 Summary of logistic regression models used to estimate probability of presence of Roanoke logperch in microhabitat and mesohabitat locations in the Roanoke and Nottoway rivers, Virginia. Parameter estimates are maximum-likelihood estimates, and significance of each variable is based on Wald chi-square. Significance of each model is based on a chi-square of the -2 log-likelihood statistic.

Mesohabitat Models:

Roanoke River Model		(Chi-square = 30.8, df = 6, P < 0.0001)		
Variable	Parameter Estimate	Chi-square	df	P
Intercept	-11.7	9.1	1	0.003
Pool (class variable)	-2.6	6.3	1	0.01
Riffle (class variable)	1.5	5.6	1	0.02
Dominant Substrate (rank)	0.83	5.1	1	0.02
Subdominant Substrate (rank)	0.89	7.0	1	0.008
Silt (rank)	-0.86	4.6	1	0.03
Total woody debris	-0.32	3.1	1	0.08

Nottoway River Model		(Chi-square = 15.5, df = 3, P = 0.001)		
Variable	Parameter Estimate	Chi-square	df	P
Intercept	-0.82	1.4	1	0.23
Distance to like habitat	-0.0008	3.3	1	0.07
Subdominant Substrate	-0.29	5.1	1	0.02

Microhabitat Models:

Roanoke River Model		(Chi-square = 38.5, df = 6, P < 0.0001)		
Variable	Parameter Estimate	Chi-square	df	P
Intercept	-7.0	31.2	1	< 0.0001
Depth (cm)	0.01	7.1	1	0.008
Mean velocity (m/s)	8.6	10.8	1	0.001
Dominant substrate (rank)	0.25	4.0	1	0.04
Silt (rank)	0.42	6.7	1	0.01
Average velocity*Dominant substrate	-0.49	6	1	0.15
Average velocity*Silt	-0.84	3.8	1	0.05

Nottoway River Model		(Chi-square = 29.6, df = 4, P < 0.0001)		
Variable	Parameter Estimate	Chi-square	df	P
Intercept	-9.2	33.3	1	< 0.0001
depth (cm)	0.02	17.5	1	< 0.0001
Mean velocity (m/s)	-1.3	1.8	1	0.18
Dominant substrate (rank)	0.14	2.6	1	0.11
Silt (rank)	0.88	9	1	0.003

Table 2.9 The sensitivity (ability to detect presence; “# of true presences” / [“# of true presences” + “# of false absences”]) and specificity (ability to detect absence; “# of true absences” / [“# of true absence” + “# of false presences”]) of logistic regression models developed to predict the presence of Roanoke logperch in the Roanoke and Nottoway rivers, Virginia, using mesohabitat (A) and microhabitat (B) use data. Underlined values indicate model verification. The remaining values indicate the transferability of models between rivers.

(A)
Mesohabitat Models
 Sensitivity/ Specificity

Data Source for logistic regression models		
Models transferred to:	Roanoke River	Nottoway River
Roanoke River data set	<u>0.75/ 0.81</u>	0/ 0.61
Nottoway River data set	0/ 0.88	<u>0.73/ 0.65</u>

(B)
Microhabitat Models
 Sensitivity/ Specificity

Data Source for logistic regression models		
Models transferred to:	Roanoke River	Nottoway River
Roanoke River data set	<u>0.93/ 0.43</u>	0.02/ 0.98
Nottoway River data set	0.97/ 0.29	<u>0.57/ 0.84</u>

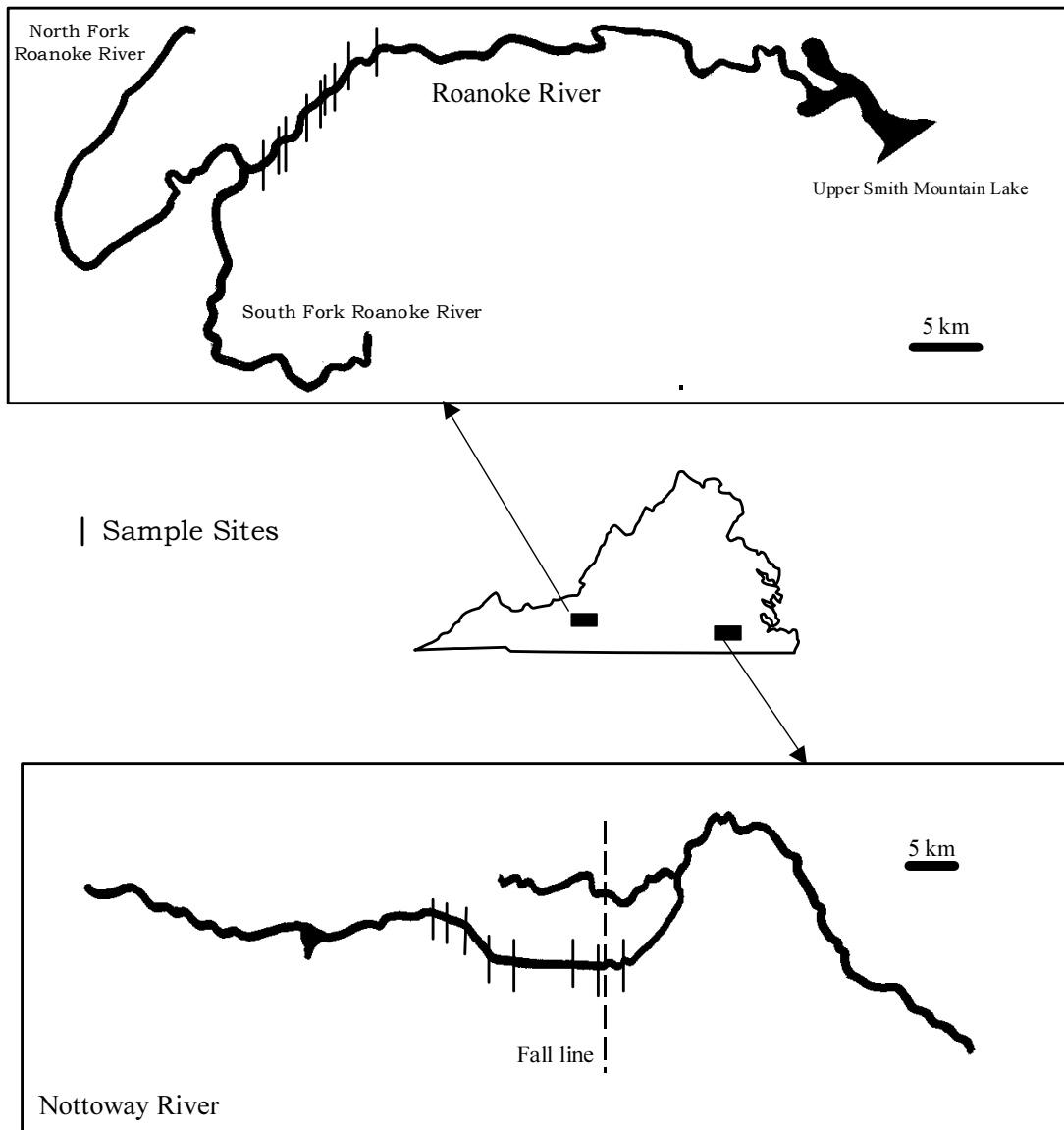


Figure 2.1 Map of the Roanoke and Nottoway rivers, Virginia, indicating sites selected for snorkeling surveys for Roanoke logperch (*Percina rex*).

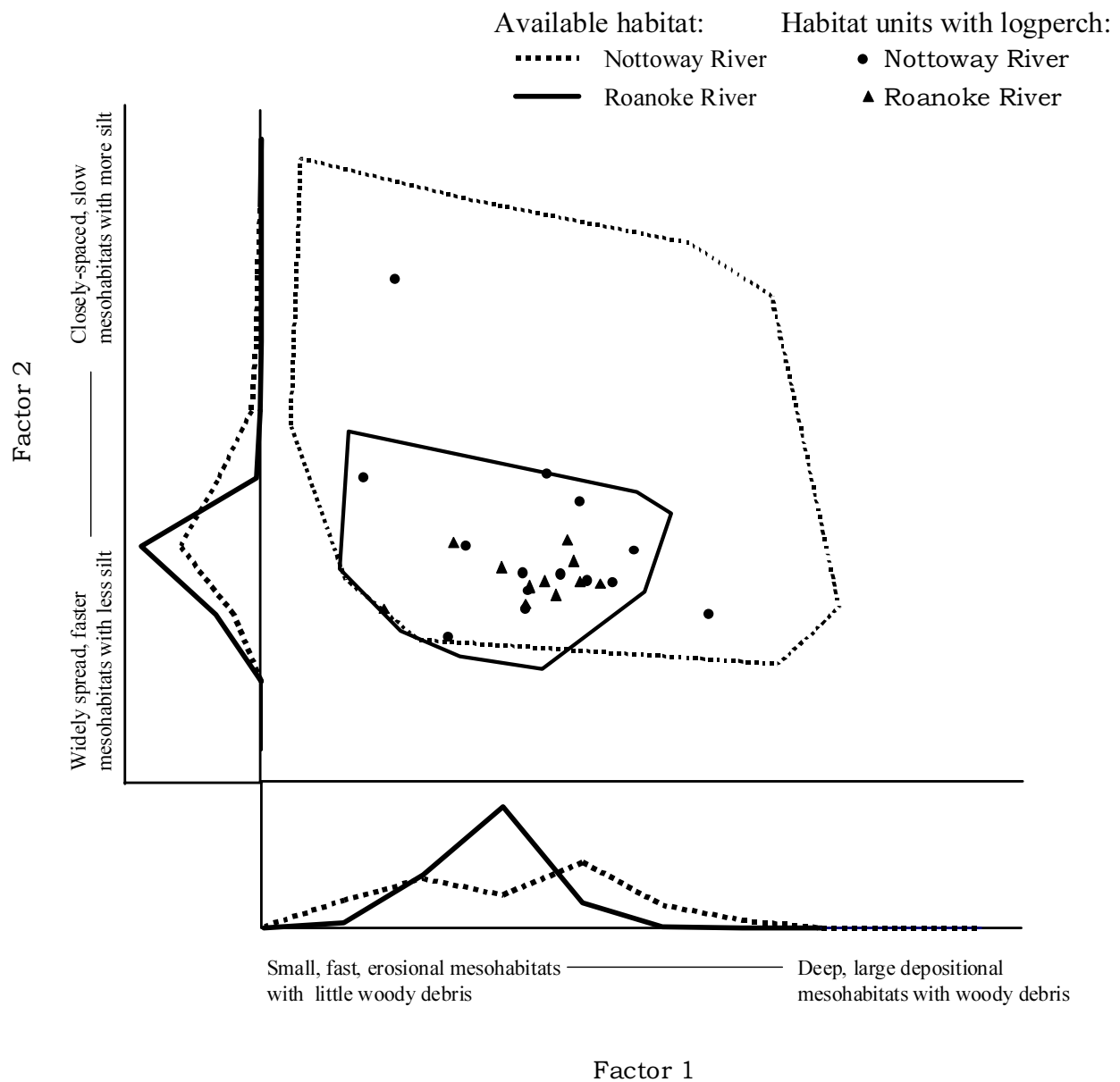


Figure 2.2 A graphic presentation of principal component scores for mesohabitats containing Roanoke logperch in the Roanoke and Nottoway rivers, Virginia. The polygon in each figure circumscribes the area representing available mesohabitats in each system, while the area curves next to the axes represent the relative frequency of mesohabitat availability locations.

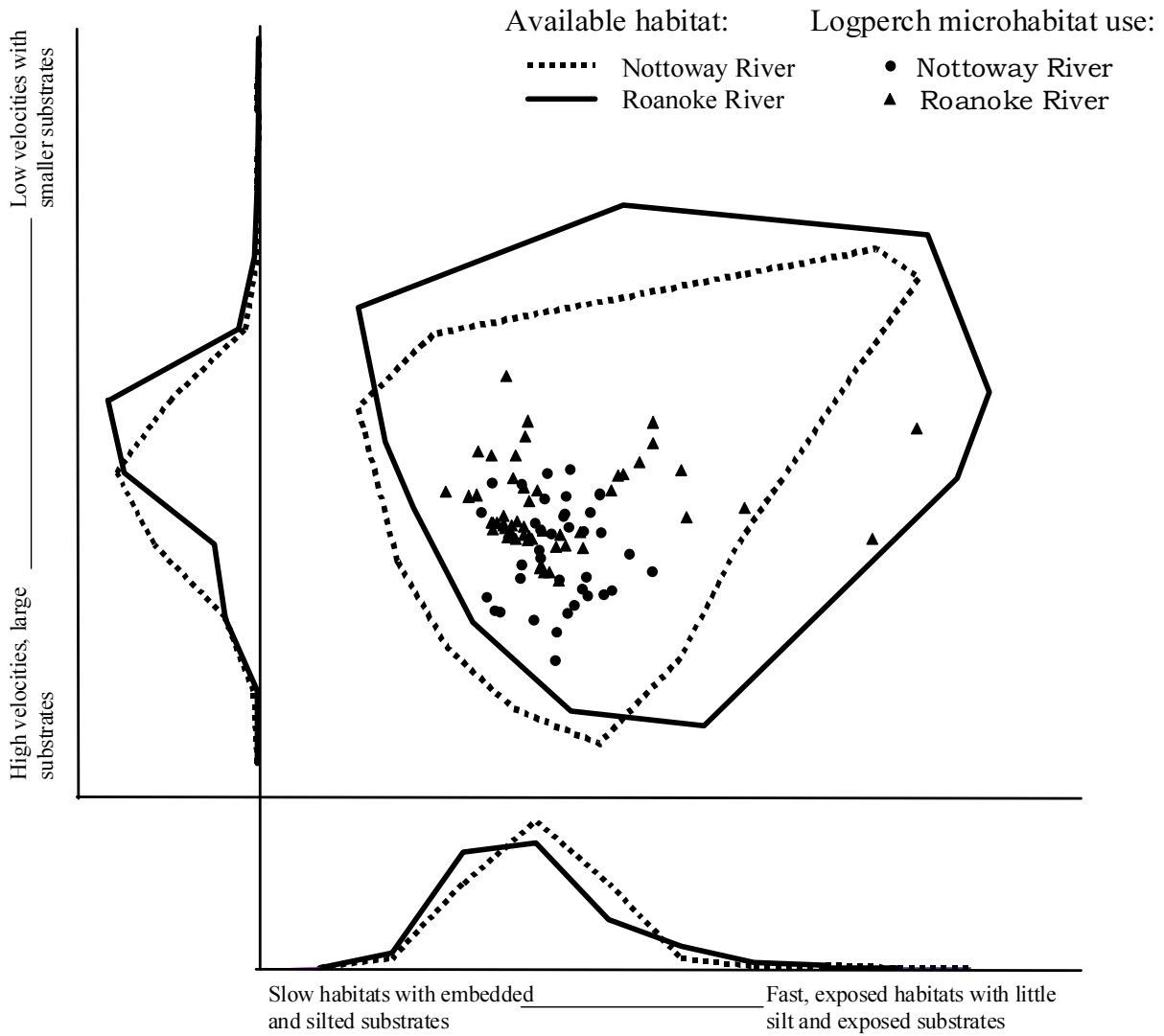


Figure 2.3 A graphic presentation of principal component scores for microhabitat locations where Roanoke logperch were observed in sites surveyed in the Roanoke and Nottoway rivers, Virginia. The polygon in each figure circumscribes the area representing available microhabitat in each system, while the area curves next to the axes represent the relative frequency of microhabitat availability locations.

Chapter 3. Ontogenetic shifts in habitat use by the endangered Roanoke logperch (*Percina rex*)

INTRODUCTION

Among the most difficult and pressing goals of conservation biology is the preservation and restoration of aquatic biodiversity amidst rapid and pervasive human impacts on aquatic resources (Etnier 1997, Richter et al. 1997, Williams et al. 1997). Degradation of aquatic ecosystems through habitat loss, introduction of nonnative species, sedimentation, and pollution has contributed to high endangerment and extinction rates among aquatic species (Miller et al. 1989, Williams et al. 1989, Williams et al. 1993, Etnier 1997), potentially three to eight times the rates for terrestrial birds and mammals (Master 1990). Of 490 fish species native to the southeastern United States, 19% are considered jeopardized (Etnier 1997). Benthic stream fishes that require silt-free habitat are particularly vulnerable to human impacts (Etnier 1997). To reverse declines and restore populations of imperiled species, aquatic resource managers must understand habitat requirements over life histories as well as ecosystem-level processes that maintain these habitats (Schlosser and Angermeier 1995, Labbe and Fausch 2000).

Most management strategies for imperiled stream fishes are based on knowledge of adult habitat use because juveniles and larvae can be difficult to identify and observe using standard survey techniques. This can prove problematic, particularly because stream fish populations may be most limited by breeding and rearing conditions (Berkman and Rabeni 1987), and because a variety of habitat types is required over life history for population persistence (Schlosser and Angermeier 1995, Labbe and Fausch 2000). Many studies of fishes have documented shifts in habitat use over ontogeny (e.g., Magnan and Fitzgerald 1984, Werner and Gilliam 1984, Schlosser, 1987, 1988, Werner and Hall 1988, L'Abée Lund et al. 1993, Ruzycki and Wurtsbaugh 1999), presumably related to differences among size or age classes in resource utilization abilities, predation risk (Kushlan 1976, Britton and Moser 1982, Power 1984, 1987, Werner and Gilliam 1984, Mahon and Portt 1985, Schlosser 1987, 1988, Werner and Hall 1988), or tolerance of physiological stressors (Tramer 1977, Mann and Bass 1997). Effective conservation must, therefore, account for habitat use over the entire life cycle of the target species. Repeated studies have demonstrated that population bottlenecks often occur during the

earliest stages in fish life histories (see review by Werner and Gilliam 1984). In addition, juvenile and larval fishes can be the best indicators of ecological function (Copp et al. 1991), community composition, and habitat complexity (Marchetti and Moyle 2000). Early life stages of fishes are particularly vulnerable to human alterations of stream systems, including sedimentation (Burkhead and Jelks 2001) and channel modification or flow regulation (Scheidegger and Bain 1995, Copp 1997, Mann and Bass 1997, Mérioux and Ponton 1999, Meng and Matern 2001).

The spatial structure of lotic systems can be viewed hierarchically, from microhabitats to drainage basin units (Frissel et al. 1986). Within regional distributions of fish assemblages (e.g., drainage and/or physiography), numerous local factors, some relating directly to regional conditions, can determine the distributional limit of a species. Fish species have been found to respond to habitat features at multiple scales, particularly through movement of different life history stages to suitable habitat patches (Labbe and Fausch 2000). My study focuses on habitat requirements through ontogeny for an imperiled species at smaller scales (i.e. reaches, pool-riffle series, and microhabitat). Knowledge of habitat use at this scale can be used to make management decisions geared towards preservation of the larger processes that create required habitat patches. Comparing habitat use over ontogeny and between populations can give insight to limiting factors and generalities for the species as well as its ability shift habitat use under different regional conditions.

The Roanoke logperch (*Percina rex*) is a large darter that occurs only within the Roanoke and Chowan drainages of Virginia (Jenkins and Burkhead 1993). Its greatest population densities are in the upper Roanoke River (Burkhead 1983, Jenkins and Burkhead 1993) and in the Nottoway River drainage (tributary to the Chowan River) along the fall zone between the Piedmont and Coastal Plain physiographic provinces (Rosenberger and Angermeier 2002). Based on its limited distribution and the vulnerability of its largest population centers to urban and industrial stressors, Roanoke logperch are federally endangered (Federal Register Vol. No. 159).

Current understanding of logperch life history is described in Burkhead (1983) and Jenkins and Burkhead (1993) and is based exclusively on data collected in the Roanoke River. Adult logperch in the Roanoke River typically are found in deep, high velocity riffle and run habitats, while young and juveniles have been observed in slow runs and pools, where they are

frequently observed over clean sand bottoms (Burkhead 1983). Standard electrofishing techniques collect very small logperch inefficiently. Over the duration of his two-year study, Burkhead (1983) observed only two young-of-year (YOY) in shallow, sandy pool margins in the Roanoke River. Roanoke logperch of all age classes seem intolerant of moderate to heavily silted substrates in the Roanoke River, possibly due to the feeding behavior unique to the subgenus *Percina*. Logperch use their conical snout to flip gravel and feed on exposed invertebrates. This exposes prey sheltered beneath rocks that may otherwise not be available to other benthic fishes; however, this feeding behavior relies on the availability of loosely embedded substrate (Burkhead 1983, Jenkins and Burkhead 1993).

Outside of the Roanoke River, habitat use by other populations of logperch differs to some degree (see Chapters 1 and 2). Differences in habitat availability between these rivers may influence ontogenetic patterns of habitat use. The Roanoke River is a clear, coolwater, high gradient system, while the Nottoway River in the Chowan drainage is tannin-stained, warmwater, and lowland (Jenkins and Burkhead 1993). The Nottoway River is similar in gradient to the Roanoke River only in the Fall Zone between the Piedmont and Coastal Plain physiographic provinces, where riffle and run habitat similar to that in montane rivers occur. Studies have demonstrated differences in habitat use for different populations of a fish species (Bozek and Rahel 1992, Freeman et al. 1997), particularly populations from different regions (Groshens and Orth 1994). Therefore, a comparison of ontogenetic shifts between the rivers will offer insights on ultimate factors determining habitat use patterns in the two systems.

OBJECTIVES

The purpose of this study was to document and quantify ontogenetic shifts in habitat use by the federally endangered Roanoke logperch in the Roanoke and Nottoway rivers. I examine the habitat use of individual Roanoke logperch in three size categories in the Roanoke River and in two size categories in the Nottoway River to determine whether: 1) age classes of logperch exhibit habitat selectivity, 2) age classes differ in habitat use, and 3) ontogenetic patterns of habitat use differ between the Roanoke and Nottoway populations. I use these results to generate hypotheses on what factors may cause shifts in habitat use through Roanoke logperch ontogeny in both river systems. I discuss the relative importance of these factors in the two river

systems and use commonalities in habitat use between the two rivers to form generalized hypotheses about the habitat requirements of this species. Comparison of habitat availability between rivers gives insight into mechanisms contributing to differences in habitat use between the Roanoke and Nottoway rivers. Finally, I discuss conservation and management implications of those ontogenetic habitat shifts and suggest strategies that will preserve habitat mosaics required through Roanoke logperch life history for both populations.

METHODS

Study sites

The section of the upper Roanoke River targeted by this study extends downstream from the confluence of the North and South forks. The section of the Nottoway River targeted for this study crosses the Fall Line between the Piedmont and Coastal Plain physiographic provinces (Figure 3.1). Fish sampling in both rivers was conducted during the summers of 2000 and 2001. I examined habitat use at small scales (i.e., pool-riffle series and microhabitat), where processes such as alluvial transport of water and sediment, presence of woody debris, channel meandering, and animal activity (e.g. beaver, cow) can affect habitat availability (Frissel et al. 1986). In the summer of 1999, a reachwide inventory of 10km of the Roanoke River and 22km of the Nottoway River was conducted using the Basinwide Visual Estimation Technique (BVET; Dolloff et al. 1993). Riffle:run:pool series were systematically selected from these reachwide inventories for quantitative underwater observation for adult and subadult logperch using line transect snorkeling methods. I considered high gradient areas with convex stream bottoms, turbulent water surfaces, and fast water to be riffle habitat. Pools were deep, low gradient, slow-moving areas with concave stream bottoms (following Beschta and Platts 1986). Runs were defined as intermediate gradient areas with flat stream bottoms, fast water, and smooth water surfaces (Vadas and Orth 1998). Once methods were established for YOY observations, a 2-km stretch of the Roanoke River was selected for visual survey (Figure 3.1). This stretch was selected based on river access and was centrally located along the inventoried river reach. Due to logistic and time constraints, I did not attempt to visually survey habitats for YOY logperch in the Nottoway River.

Fish Survey Methods

Standard survey observations for each riffle:run:pool series were made via line-transect snorkeling methods described in Ensign et al. (1995). One to three parallel lines oriented with river flow were marked with yellow line on the day of sampling. Spacing between lines was a minimum of 1.5 times maximum underwater visibility on the day of sampling. The length of the lines was based on the length of the habitat units but did not exceed 50m per unit (150m per site). Visibility was determined by suspending a Secchi disk in the water column in front of a snorkeler. The snorkeler moved away from the disk until the black patterns on the disk were no longer distinguishable from the water. The distance between the snorkeler and the disk was measured and served as the maximum visibility for that day. Fish sampling was not conducted if maximum visibility was less than 1.5 meters (from Leftwich et al. 1997).

To minimize effects on fish behavior, snorkelers did not begin sampling until at least one hour after placement of the transect lines. Snorkelers entered the water downstream of the area to be sampled and moved slowly upstream along the lines, keeping the center of the body over the line. Each observer scanned the stream bottom, mid-water, and upper-water column directly in front and to both sides of the line of travel. When a logperch was sighted, a numbered weighted marker was placed on the stream bottom precisely where the fish was first spotted. The number-codes of markers and size class were recorded on dive slates. Double counting of fish was avoided by simultaneously sampling all three transect lines with snorkelers staying even with each other while moving upstream. Continuous communication between snorkelers also minimized double counting. After the pool-riffle-run sequence was sampled, snorkelers returned to the base of transects to count markers and collect habitat data.

Habitat observations

Microhabitat data included water depth, bottom and mean water velocity, substrate size (using a 9-category Wentworth scale), embeddedness within a 1-m² area around the marker (1 = 95% embedded, 2 = 50-94%, 3 = 25-49%, 4 = 1-24%, 5 = 0%, i.e. exposed), and silt cover within a 1-m² area around the marker (1 = 76-100% covered with silt, 2 = 51-75%, 3 = 26-50%, 4 = 1-25%, 5 = 0%). Microhabitat availability was recorded within 24 hours of the snorkeling run. Horizontal transects along the wetted width of the river were placed at 10-meter intervals along

the length of the pool-riffle-run series. Every three meters on the horizontal transect, depth, mean and bottom water velocity, silt cover, and dominant and subdominant substrate within a 1-m² area are recorded. In addition, rank predator abundance in pools, riffles, and runs was estimated after the snorkeling run (1 = absent, 2 = rare, 3 = uncommon, 4 = common, 5 = abundant). Predators observed in the Roanoke River included small and largemouth bass (*Micropterus dolomieu* and *M. salmoides*) and rock bass (*Ambloplites rupestris*). Smallmouth and largemouth bass, longnose gar (*Lepisosteus osseus*), bowfin (*Amia calva*), Roanoke bass (*Ambloplites cavifrons*), and American eels (*Anguilla rostrata*) were observed in the Nottoway River.

YOY logperch (< 4cm total length; TL) were not observed during snorkeling surveys. To observe YOY logperch, 2-3 researchers used polarized glasses and binoculars to survey shallow waters associated with backwaters, secondary channels, and river edges. When an individual or group of YOY fish was observed, the surveyor identified any logperch and placed markers on spots that small logperch were seen foraging. Habitat use and availability data were recorded at the site where each fish was observed using a cross-shaped transect, which was centered on the logperch sighting location (Figure 3.2). Habitat data were taken along transect arms set at 45°, 135°, 225°, and 315° from this center sighting location. Habitat availability was measured in each transect line 1, 1.5, 2.0, and 3.0 meters from the center point. The following habitat variables were recorded: depth, mean and bottom water velocity, embeddedness and silt cover in a 10-cm² area, and substrate size over which the YOY was observed. Data collection methods for adults and subadults differed from data collection for YOY individuals primarily in their scale of measurement (i.e. extent and grain). I presumed that small individuals perceive and use habitat at a smaller scale than do larger individuals, justifying comparison among data sets for a subset of the microhabitat measurements.

Data Analysis

All data analyses were performed using SYSTAT (Version 9, Copyright © SPSS Inc., 1998). Habitat availability data collected in the Roanoke and Nottoway rivers include water depth (cm), bottom and mean water velocity (m/s), dominant substrate (rank category), embeddedness (rank category), silt cover (rank category), and predator abundance (rank category). Availability data were separated into pool, riffle, and run habitat unit categories to

examine differences in mesohabitat characteristics between the two rivers. Univariate *t*-tests were used for comparison between the two rivers for depth, bottom velocity, and mean velocity. Ranked (discrete) measurements violated normality assumptions; therefore, I performed nonparametric Mann-Whitney *U* tests to compare substrate, embeddedness, silt, and predator abundance between Roanoke and Nottoway river pools, riffles, and runs. Alpha values were adjusted for multiple tests using the Dunn-Sidak correction ($\alpha'=0.02$). Because habitat use by logperch is likely based on interacting factors, it is meaningful to address habitat questions with a multivariate approach. Differences between pools, riffles, and runs in the two rivers in microhabitat availability were determined using multivariate analysis of variance (MANOVA, SYSTAT).

Microhabitat use data included mean velocity (m/s), bottom velocity (m/s), substrate (rank category), embeddedness (rank category), silt cover (rank category), and depth (cm). Logperch were segregated into three age categories based on Burkhead (1983). Individuals < 4cm were classified as YOY. Roanoke logperch mature at three years (8-11.4 cm TL, Burkhead 1983); therefore individuals between 4cm and 8cm TL were considered subadults between the ages of 1 and 2, and individuals > 8cm TL were considered adults between the ages of 3 and 6. *G*-tests with Williams' correction (Williams 1976) were used to detect habitat selection by each age class by comparison of actual habitat use with that expected if logperch used habitat randomly. Category ranges were selected such that each category was equally available in a given river; thus categories differed among rivers. Alpha values were adjusted for multiple tests using the Dunn-Sidak correction ($\alpha'=0.02$). Differences among age classes for each habitat parameter were tested with Kruskal-Wallis tests for the Roanoke River and Mann-Whitney-*U* tests for the Nottoway River. After verification of linearity assumptions, multivariate comparison of logperch habitat use with available habitat was examined with principal components analysis (PCA). In addition, PCA was used to indicate marked differences among age classes in habitat use. Differences among age classes in habitat use were quantitatively examined with multivariate analysis of variance (MANOVA) and discriminant analysis (SYSTAT).

RESULTS

Habitat use descriptions

Adult logperch in the Roanoke River were observed most frequently in runs, occasionally in riffles, and rarely in pools (Table 3.1). Within habitat units, adult logperch primarily use deep water, medium- to high-water velocities, often directly over gravel substrate in areas dominated by cobble. Subadults in the Roanoke River were observed primarily in runs over moderately embedded gravel in slightly shallower and lower velocity habitats than the adults. Subadults were occasionally observed in riffles and pools. Logperch less than 4cm TL, in contrast, were found in nearly stagnant areas such as backwater habitats; secondary channels, and the shallow edges of pools, riffles, and runs. These small individuals consistently were found in water around 20 cm deep with small, slightly embedded substrate. A heavy silt blanket covered these areas; however, small logperch foraged in small patches of silt-free, loosely embedded gravel. Adult and subadult logperch in the Roanoke River did not exhibit schooling behavior, but YOY logperch were observed in mixed-species schools. These mixed schools included unidentified YOY cyprinids and *Hypentelium* spp. Small logperch occasionally separated from schools to feed, flipping small gravel. I was unable to observe whether these foraging attempts were successful.

Adult and subadult logperch in the Nottoway River were observed primarily in pools and occasionally in runs. Few adults and no subadults were observed in riffle habitat (Table 3.1). Both adult and subadult logperch in the Nottoway River were found over sand and gravel in deep, low velocity habitats. Although both age classes were found over relatively exposed and lightly silted habitats, the subadults were found in slightly more silted habitat with lower velocities. Unlike the Roanoke River, subadults were observed frequently in the Nottoway River (Table 3.1).

Univariate analysis

Habitat availability differed between the Nottoway and Roanoke river pools, riffles, and runs (Table 3.2). For all unit types, the Nottoway River was consistently deeper ($t > 2.8$, $P < 0.005$), less embedded, and less silted (Chi-square > 20.7 , $P < 0.001$) than the Roanoke River. Nottoway River pools and riffles had wider channels than corresponding units in the Roanoke

River ($t > 3.2$, $P < 0.001$). Substrate sizes were smaller in Nottoway River runs and pools than what was observed in the Roanoke River (Chi-square > 25.8 , $P < 0.001$). I did not detect any differences between rivers in run, riffle, and pool predator abundance (Chi-square < 0.14 , $P > 0.71$). Multivariate habitat availability for all unit types differed significantly between the Roanoke and Nottoway rivers (Wilks' lambda > 0.66 , $F > 13.1$, $df = 7$, $P < 0.001$).

Habitat selectivity by logperch varied among age classes and habitat parameters, as well as between rivers. All age classes of logperch non-randomly selected for depth in the Roanoke River ($G \geq 10.0$, $df = 3$, $P < 0.01$, Figure 3.3). Adults selected deeper habitats, while subadults selected intermediate depths. YOY consistently selected water depths between 16 and 30 cm. All age classes non-randomly selected for mean water velocity in the Roanoke River, with individuals proportionally skewed towards higher velocities for adults ($G = 52.9$, $df = 4$, $P < 0.001$), medium velocities for subadults ($G = 20.1$, $df = 4$, $P < 0.001$), and very low velocities for YOY ($G = 29.7$, $df = 4$, $P < 0.001$). There was no apparent selection, however, for bottom water velocity by any age classes ($G \leq 7.1$, $df = 3$, $p < 0.10$). Adults and subadults selected substrates ranging from sand to cobble ($G \geq 11.2$, $df = 3$, $P < 0.02$), while YOY selected smaller substrate categories (sand and small gravel, $G = 46.1$, $df = 3$, $P < 0.001$, Figure 3.3). Adults and YOY selected for moderately embedded to exposed substrate with little silt ($G \geq 16.6$, $df = 4$, $P < 0.005$). No apparent selection for embeddedness or silt categories was observed in subadults in the Roanoke River ($G \leq 10.3$, $df = 4$, $P > 0.05$), though no age classes were observed in severely embedded or heavily silted substrate.

In the Nottoway River, both adult and subadult logperch selected for deep-water habitats ($G \geq 13.0$, $df = 5$, $P < 0.02$, Figure 3.3). However, age classes selected different mean water velocities, with adults selecting moderately fast water ($G = 16.1$, $df = 5$, $P < 0.01$) and subadults selecting slow water ($G = 32.2$, $df = 5$, $P < 0.001$). Despite these differences, both age classes selected slow bottom velocities ($G \geq 11.3$, $df = 3$, $P < 0.01$). Adults selected substrate suitable for feeding (gravel or cobble) and sand, the most common substrate category in the Nottoway River ($G = 10.1$, $df = 3$, $P = 0.02$). Subadults did not appear to select for substrate category, though individuals frequently were observed over sand and gravel ($G = 6.46$, $df = 3$, $P > 0.1$). Adults and subadults were frequently observed flipping small pieces of organic debris when foraging over sand. Adults and subadults did not appear to select for embeddedness ($G \leq 6.8$, df

= 4, $P > 0.1$); however, both adults and subadults selected habitat with little to no silt cover ($G \geq 16.9$, $df = 4$, $P < 0.005$).

Kruskal-Wallis tests indicated that adult logperch use deeper, faster water than subadults and YOY in the Roanoke River (Chi square ≥ 44.7 , $df = 2$, $P < 0.001$). Roanoke River subadults were found in intermediate depths when compared to adults and YOY (Chi square ≥ 44.7 , $df = 2$, $P < 0.001$) and used more deeply embedded habitats (Chi square = 9.8, $df = 2$, $P = 0.008$, non-parametric multiple comparisons, $\alpha \leq 0.05$, Figure 3.4). No significant differences among age classes in median habitat characteristics were observed for substrate size, silt cover, and bottom water velocity in the Roanoke River (Chi-square ≤ 8.05 , $df = 2$, $P \geq 0.02$).

As in the Roanoke River, Nottoway River logperch adults were found in faster velocities than subadults (Chi-square = 18.3, $P < 0.001$). In addition, adults were found in less silted habitats than subadults (Chi-square = 13.2, $P < 0.001$, Figure 3.4). No significant differences among age classes in median habitat characteristics were observed for depth, bottom velocity, substrate, and embeddedness in the Nottoway River (Chi-square ≤ 0.65 , $P > 0.42$).

Multivariate analysis

Habitat use and availability locations in the Roanoke River ordinated through PCA into two primary principal components (Table 3.3). The first component was loaded heavily by embeddedness, silt, substrate, and mean and bottom water velocities, while the second component was loaded most heavily by depth. One end of the first axis (component 1) represents stagnant, embedded habitats with small substrates, while the other end represents scoured habitats with larger substrate and high water velocities (Figure 3.5). The two ends of the second axis indicate shallow versus deep habitat.

Plots of logperch locations in the Roanoke River onto two-dimensional principal component space illustrate patterns of habitat selection when superimposed on the range of locations representing available habitat (Figure 3.5). Segregation among age classes is most marked along the second axis, representing depth characteristics; however, adult logperch span a greater range of velocity, substrate, embeddedness, and silt characteristics and occupy the more scoured and fast-flowing habitats than other age classes (Figure 3.5). Frequency distributions of habitat availability locations along the two axes indicate that scoured and fast-flowing habitat locations are the most rare habitats in sites in the Roanoke River. Although logperch locations

do not occupy habitat “extremes” along the axis, all age classes combined occupy a large portion of available habitat, indicating that a wide range of habitat types, both common and rare, is used by Roanoke logperch in the Roanoke River through ontogeny (Figure 3.5).

PCA illustrated different patterns of ontogenetic habitat use in the Nottoway River than in the Roanoke River. Habitat use and availability locations ordinated into two primary principal components (Table 3.3). The first component was loaded heavily by velocity characteristics, silt, and embeddedness, while the second component was loaded most heavily by bottom velocity and substrate. The ends of the first axis (component 1) represent stagnant, embedded habitats with silt cover versus high velocity, scoured habitats. The extremes in the second axis (component 2) represent fast bottom velocity habitats with small substrate versus slow bottom velocity habitat with large substrate (Figure 3.5). Although presence of low bottom velocities and large substrate seems counter-intuitive, it follows that smaller substrates, such as sand, create a smaller velocity boundary layer than larger substrates. Adults were skewed towards the high velocity, scoured extreme of axis 1, while subadults seemed to occupy more low velocity habitats; however, there is considerable overlap between age classes. As was observed in the Roanoke River, logperch did not occupy “extremes” along either axis. Relative frequency of habitat availability locations along the two principal axes indicate that logperch occupy habitat configurations that are common in Nottoway River sites.

Multivariate habitat use differed significantly through logperch ontogeny in the Roanoke River (Wilks' lambda = 0.26, $F = 11.5$, $df = 12$, $P < 0.001$). Further, plots of discriminant analysis scores of the three age classes indicate segregation among logperch age classes in habitat use (Figure 3.6). The first discriminant axis is loaded primarily by variation in water depth and silt cover, while the second axis is most heavily loaded by embeddedness (Table 3.4). The canonical scores plot confirms univariate analyses, indicating that age classes in the Roanoke River separate most markedly by depth and velocity, and subadult locations are more embedded than adult and YOY locations (Figure 3.4 and 3.6).

Although subadult and adult logperch differ significantly in multivariate habitat use in the Nottoway River (Wilks' lambda = 0.67, $P < 0.001$), differences are subtle when compared to the Roanoke River. Subadults and adults are significantly different only along one discriminant axis (Figure 3.7), which is loaded most heavily by velocity and silt (Table 3.4). Again, this follows

univariate analyses for the Nottoway River, with adults occupying locations with faster velocities and lower silt cover than subadults.

DISCUSSION

Ontogenetic shifts in habitat use

Roanoke logperch appear to select specific habitat configurations and use a wide range of habitats in the Roanoke and Nottoway rivers through ontogeny. In the Roanoke River, adult logperch select deep, high velocity riffles and runs, which provide loosely embedded substrate for feeding and potential spawning habitat (Burkhead 1983). Subadults in the Roanoke River, however, are found in habitats intermediate in depth, with lower velocities, greater silt loads, and moderately embedded substrate. YOY logperch also were found in low-velocity habitat, yet were not observed in the river thalweg. Instead, small individuals were found in shallow backwaters and river edges feeding over small patches of loosely embedded, silt-free gravel substrate. Adult and subadult Roanoke logperch in the Nottoway River are found primarily in deep, silt-free, low velocity pools with sand and gravel substrate and occasionally in runs and riffles. As in the Roanoke River, adult logperch in the Nottoway River were found in faster water velocities than subadults, corresponding with slightly less silted substrate.

The ontogenetic shifts in habitat that I observed in the Roanoke and Nottoway rivers may be related to a variety of factors that affect individual survival, growth, and reproductive success; constraints related to these parameters are likely to change through ontogeny (Werner and Gilliam 1984, Schlosser, 1987, 1988). Predator-prey interactions associated with different habitat types, among other factors, could play a key role in variation in habitat use over body size (Angermeier 1992). Fish have low costs of maintenance and can handle some degree of starvation in order to avoid predators; therefore, predation may be more immediately important than food for habitat selection (Power 1984); however, this relationship can be dynamic because fishes can facultatively change feeding rates in response to changes in predation risk (Werner and Hall 1988). Hypotheses relating habitat use to predation risk generally state that risk in shallow habitats is from non gape-limited predators (e.g., wading or diving birds), while risk in deep habitats is mostly from gape-limited predators (e.g., piscivorous fishes; Magalhães 1993, Angermeier 1992, Schlosser 1987, 1988, Power 1984). Large predatory fish are rarely observed

foraging in shallow water, potentially due to risk of aerial predation or decreased maneuverability (Angermeier 1992). In addition, Schlosser (1987) found in an artificial stream that small juvenile and adult fishes are constrained to shallow riffle/raceway habitat when predators are in pools, but, without predators, all taxa preferred structurally complex or simple pools, even at the cost of low food availability. However, small YOY, though vulnerable to a variety of aquatic predators, are less likely to be preyed upon by wading or flying predators than larger individuals (Kushlan 1976).

Other habitat-related factors that may play a role in shifts over ontogeny include competition and swimming ability. Evidence for the importance of competition in habitat associations for darter species (Percidae) has been varied, and studies have been confined to comparisons between species (Greenberg 1988, Schlosser and Toth 1984). These studies indicated that shifts in habitat use by darters are more likely related to fluctuations in habitat availability rather than species interactions (Schlosser and Toth 1984, Greenberg 1988). Finally, body size has been directly related to the ability of fishes to maintain position under high water velocities (Mann and Bass 1997), with larger individuals having greater swimming abilities than small individuals. This phenomenon has been observed in juveniles of fantail darters (*Etheostoma flabellare*) in the Roanoke River (Matthews 1985).

These findings may shed light on mechanisms for ontogenetic habitat preferences of Roanoke logperch in the Roanoke River. For adult logperch, deep, turbulent, and fast riffle and run habitats may be silt-free refugia from aquatic and aerial predators. Subadult logperch, however, may be unable to exploit these high velocity areas due to limited swimming ability. Subadults in the Roanoke River were observed in runs and riffles of intermediate depth and velocity, corresponding with an increase in substrate embeddedness. A slight shift into shallower waters may be a defense against predation; however, complicating this mechanism of depth stratification of logperch is the distribution of heavily silted substrate in the Roanoke River. Habitats with slow water velocities (i.e., pools) are heavily silted (Table 3.2). Aquatic predators also inhabit these areas; therefore, it is difficult to separate the effects of predation from the effects of heavy silt on depth and velocity preferences of subadult Roanoke logperch. Shallow backwaters habitats may provide slow water velocities and refugia from aquatic predators; however, subadults may be too large to use these areas effectively. In backwaters, subadults may be vulnerable to aerial predation. In addition, these areas were covered with a

thick blanket of silt with the exception of very small areas of loosely embedded small gravel that are probably too small to be used by subadult logperch.

YOY logperch in the Roanoke River may find refugia from large, gape-limited predators in backwaters and unit edges and, due their small size, are unlikely targets of wading predators (Kushlan 1976). They are also small enough to forage in small patches of loosely embedded, silt-free gravel available in these habitats. The schooling behavior of young logperch in these shallow areas indicates some risk of aquatic predation, even in shallow waters. Ontogenetic shifts from shallow to deep water through ontogeny have been observed in other stream fishes (Magnan and Fitzgerald 1984). Nursery habitat is commonly described as shallow, off-channel habitat without velocities that would limit swimming abilities of small individuals and offer shelter from large aquatic predators (Copp 1991, 1997; Leslie and Timmins 1991; Scheidegger and Bain 1995; Baras and Nindaba 1999; Bell et al. 2001; Gadowski et al. 2001).

Roanoke logperch in the Nottoway River occupy habitat that is common and widespread in all sites selected for sampling. This is accompanied by extensive habitat use overlap between the two age classes, unlike what I observed in the Roanoke River. No segregation in depth or embeddedness characteristics was observed; however, like in the Roanoke River, adult and subadult logperch in the Nottoway River segregated by velocity. This supports the notion that subadult logperch have less ability to navigate successfully in fast-moving water than adults. This preference corresponded with a slight increase in silt cover for subadult logperch in the Nottoway River. Individuals found in deep pools in the Nottoway River often were observed near large woody debris that may have served as cover from these predators and as a source of food (Angermeier 1985).

Differences between rivers in ontogenetic shifts

Ontogenetic shifts in habitat use observed in the Nottoway River were subtle. No stratification among age classes was observed for depth or embeddedness, as was observed in the Roanoke River. In addition, multivariate analyses indicated a high degree of habitat use overlap between age classes in the Nottoway River. The lack of segregation along depth and embeddedness gradients in the Nottoway River, and the segregation that was seen in the Roanoke River, indicate that different mechanisms are at work in the two rivers.

Although mechanisms I propose regarding habitat use in the two systems remain speculative, comparison between the two rivers reveals generalities about Roanoke logperch habitat use over life history. Habitat that is free of heavy siltation and contains moderately to loosely embedded substrate is preferentially used in the two systems. Subadults in both rivers were found in slower velocity habitats than adults, indicating that water velocity may be an important limitation for this life stage. Further, low-velocity habitats such as pools in the Nottoway River appear to have a greater density of insects important in subadult diets than in analogous habitats in the Roanoke River (Rosenberger and Angermeier 2002). The length of the Nottoway River sampled in this study is in relatively pristine condition, and pools without heavy silt loads are common and available for adult and subadult logperch. It is possible that logperch prefer low velocity, deeper habitats without silt, but that type of habitat is rare in the Roanoke River. Roanoke logperch in the Roanoke River inhabit a range of habitat types from rare to relatively common (Figure 3.5). Adults, in particular, seem capable of exploiting rare habitat that is deep, fast moving, and free of silt. In contrast, Roanoke logperch in the Nottoway River occupy widespread and common habitat, accompanied by habitat use overlap between the two age classes. This indicates a potential habitat bottleneck in the Roanoke River for juvenile or subadult logperch; with their requirements for lower velocity habitats, they may be pushed into microhabitats with embedded substrate suboptimal for foraging. This hypothesis is supported by evidence that subadult logperch are less common in the Roanoke River than in the Nottoway River.

Conservation and management implications

The Roanoke logperch recovery plan (Federal Register Vol. No. 159) is based primarily on knowledge of the adult stage, ignoring potential for spatial variation in demographic or ecological processes over multiple scales. Each size class of Roanoke logperch selected particular habitat configurations, such that over the course of its life history the species used a wide range of habitats. Successful conservation of this species will involve the preservation of the ecological processes that maintain the connected habitat mosaics required over logperch life history. The distribution of habitat types and pathways of dispersal will be critical for completion of the logperch life cycle. Habitat heterogeneity at multiple scales will contribute to its continued persistence in the Nottoway and Roanoke rivers, through formation of mesohabitat

types such as backwaters, pools, riffles, and runs as well as microhabitats with large substrate, silt-free microhabitat, and intermediate water velocities.

Microhabitats that contain loosely embedded sediment free of heavy silt cover are critical for this endangered species. Management programs in the Roanoke River should include protection and restoration of the streambank from agricultural and construction practices that contribute silt loads. Scouring flow during natural flood events should also enhance habitat through removal of small sediments, particularly in backwaters that are rarely exposed to scouring water velocities. This study suggests that suitable habitat is most limited for the subadult life stage in the Roanoke River. Further research should be conducted in this river to verify this possibility. A reachwide inventory of microhabitat types would quantify how much area in the Roanoke River is suitable for each life stage. Further, a monitoring program could be conducted before and after restoration activities that reduce sediment loads in a reach of the Roanoke River. This program could examine if area of suitable subadult habitat and subadult numbers increase after habitat enhancement. Management of Roanoke logperch in the Nottoway River should concentrate on preventative programs to preserve high quality habitat available in this river system. Historic and ongoing floodplain development, especially in the Roanoke River, can threaten logperch habitat, particularly backwaters and shorelines that appear to be important for YOY logperch. Evidence that Roanoke logperch require a low-silt, complex habitat mosaic over multiple spatial scales indicates that reach-specific management approaches alone will not ensure the recovery and persistence of this species in the Roanoke and Nottoway Rivers. I instead recommend a watershed-level approach that addresses sediment loading and preserves natural flow regimes that provide the ephemeral, seasonal, and persistent types of habitat required over logperch life history.

Table 3.1 Habitat use by Roanoke logperch and available habitat in the Roanoke and Nottoway rivers, Virginia.

Roanoke River

	YOY	Subadult	Adult	Available Habitat
Fish length (cm)	< 4	4 - 8	> 8	
Mesohabitat unit types (% occurrence)				
Backwaters and secondary channels	100 %	0 %	0 %	
Pools	0 %	23 %	16%	
Runs	0%	54%	51%	
Riffles	0%	23%	32%	
Mean Depth (cm), SD	19.7 ± 3.4	34.2 ± 10.6	52.5 ± 12.7	40.9 ± 36.1
Mean velocity (m/s), SD	0.02 ± 0.04	0.19 ± 0.23	0.63 ± 0.70	0.21 ± 0.38
Mean bottom velocity (m/s), SD	-0.01 ± 0.02	0.04 ± 0.11	0.16 ± 0.32	0.07 ± 0.21
Substrate (mean rank), SD	5.0 ± 0	6.0 ± 1.3	5.8 ± 1.7	6.3 ± 2.2
Embeddedness (mean rank), SD	3.8 ± 1.1	2.7 ± 0.95	3.7 ± 1.1	3.0 ± 1.4
Silt (mean rank), SD	4.0 ± 1	3.1 ± 1.3	3.9 ± 1.2	2.8 ± 1.6
N	17	13	49	

Nottoway River

	YOY	Subadult	Adult	Available Habitat
Fish length (cm)		4 - 8	> 8	
Mesohabitat unit types (% occurrence)				
Pools		60 %	69 %	
Runs		40 %	21 %	
Riffles		0 %	10 %	
Mean Depth (cm), SD		81.8 ± 35.7	84.4 ± 27.8	61.5 ± 36.0
Mean velocity (m/s), SD		0.07 ± 0.09	0.20 ± 0.17	0.25 ± 0.33
Mean bottom velocity (m/s), SD		0.0 ± 0.04	0.02 ± 0.09	0.06 ± 0.13
Substrate (mean rank), SD		4.9 ± 2.3	5.1 ± 2.0	5.5 ± 2.4
Embeddedness (mean rank), SD		4.0 ± 1.2	4.2 ± 1.0	3.8 ± 1.3
Silt (mean rank), SD		3.8 ± 0.9	4.5 ± 0.07	3.9 ± 1.4
N	0	40	39	

Table 3.2 Comparison of habitat characteristics of pools, runs, and riffles in the Roanoke and Nottoway rivers, Virginia. * indicates significance at the 0.02 level for t- and Mann-Whitney U tests (Dunn-Sidak correction for multiple comparisons).

POOL CHARACTERISTICS	Roanoke River	Nottoway River	t	P
Channel width (m, SD)	24.8 ± 4.3	33.1 ± 5.7	21.2	<0.001 *
Depth (m, SD)	75.7 ± 45.1	84.9 ± 35.9	2.8	0.005 *
Bottom velocity (m/s, SD)	0.06 ± 0.24	0.04 ± 0.09	1.9	0.06
Mean velocity (m/s, SD)	0.21 ± 0.45	0.15 ± 0.15	2.1	0.03
			Chi-square	P
Dominant substrate (mean rank, SD)	5.9 ± 2.5	4.7 ± 2.2	25.8	<0.001
Subdominant substrate (mean rank, SD)	4.8 ± 1.9	4.6 ± 2.4	0.57	0.45
Embeddedness (mean rank, SD)	2.5 ± 1.4	3.5 ± 1.3	78.5	<0.001
Silt (mean rank, SD)	2.4 ± 1.5	3.4 ± 1.5	62	<0.001
Predator abundance	3.4 ± 1.5	3.3 ± 1.4	0.14	0.71
			t	P
RUN CHARACTERISTICS				
Channel width (m, SD)	28.9 ± 7.8	27.8 ± 5.2	1.8	0.07
Depth (m, SD)	35.8 ± 21.16	50.7 ± 24.0	7.4	<0.001 *
Bottom velocity (m/s, SD)	0.08 ± 0.16	0.07 ± 0.13	0.73	0.47
Mean velocity (m/s, SD)	0.25 ± 0.31	0.28 ± 0.33	1.2	0.23
			Chi-square	P
Dominant substrate (mean rank, SD)	7.0 ± 1.7	5.4 ± 2.2	64.3	<0.001 *
Subdominant substrate (mean rank, SD)	5.9 ± 1.6	5.1 ± 2.1	27.5	<0.001 *
Embeddedness (mean rank, SD)	3.3 ± 1.3	3.9 ± 1.3	26.6	<0.001 *
Silt (mean rank, SD)	3.4 ± 1.4	4.3 ± 1.2	56.6	<0.001 *
Predator abundance	3.0 ± 1.4	3.1 ± 1.2	0.03	0.85
			t	P
RIFFLE CHARACTERISTICS				
Channel width (m, SD)	26.5 ± 6.1	28.9 ± 8.8	3.2	0.001 *
Depth (m, SD)	26.2 ± 16.3	34.3 ± 21.3	4.4	0.001 *
Bottom velocity (m/s, SD)	0.16 ± 0.30	0.08 ± 0.19	3.1	0.002
Mean velocity (m/s, SD)	0.40 ± 0.44	0.37 ± 0.48	0.82	0.41
			Chi-square	P
Dominant substrate (mean rank, SD)	7.7 ± 1.0	6.9 ± 2.3	0.86	0.36
Subdominant substrate (mean rank, SD)	5.7 ± 1.6	5.6 ± 2.0	0.35	0.56
Embeddedness (mean rank, SD)	3.7 ± 1.1	4.3 ± 1.1	33.2	<0.001 *
Silt (mean rank, SD)	4.0 ± 1.4	4.5 ± 1.0	20.7	<0.001 *
Predator abundance	2.0 ± 1.2	2.3 ± 1.4	0.11	0.74

Table 3.3 Loadings of six habitat variables on the first two principal components and percent of total variance accounted for by each component for the Roanoke and Nottoway rivers, Virginia.

Principal Components				
	Roanoke River, VA		Nottoway River, VA	
	1	2	1	2
Eigenvalues	2.9	1.1	2.4	1.2
Habitat Variables				
Depth	-0.228	0.748	-0.399	0.230
Bottom Velocity	0.703	0.421	0.645	-0.599
Mean Velocity	0.786	0.419	0.719	-0.378
Substrate	0.615	-0.409	0.445	0.561
Embeddedness	0.808	-0.242	0.679	0.490
Silt	0.829	-0.010	0.778	0.215
% Variance	48.0	19.0	39.3	19.3

Table 3.4 Canonical discriminant functions for two discriminant axes representing multivariate habitat use of three age classes of Roanoke logperch.

Canonical Discriminant functions

Habitat Variables	Roanoke River		Nottoway River	
	Axis 1	Axis 2	Axis 1	Axis 2
Depth	0.987	0.174	0.434	0.066
Bottom Velocity	0.027	-0.122	-0.227	0.337
Mean Velocity	0.224	-0.174	0.818	0.082
Substrate	0.259	-0.434	0.190	- 0.081
Embeddedness	-0.303	1.263	-0.563	0.063
Silt	0.534	-0.338	0.759	0.041

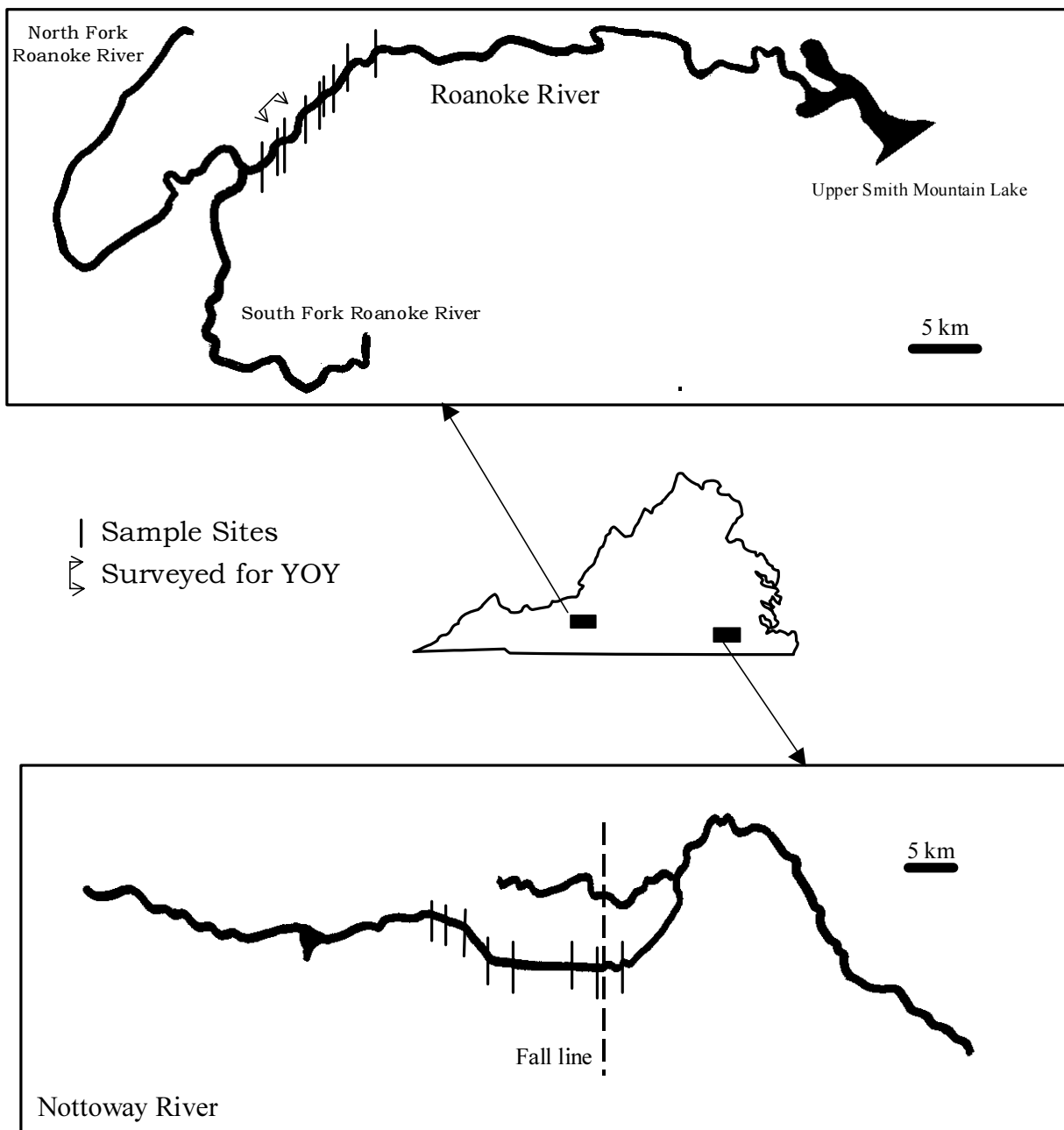


Figure 3.1 Map of the Roanoke and Nottoway rivers, Virginia, indicating sites selected for snorkeling surveys and areas surveyed for young-of-year Roanoke logperch (*Percina rex*).

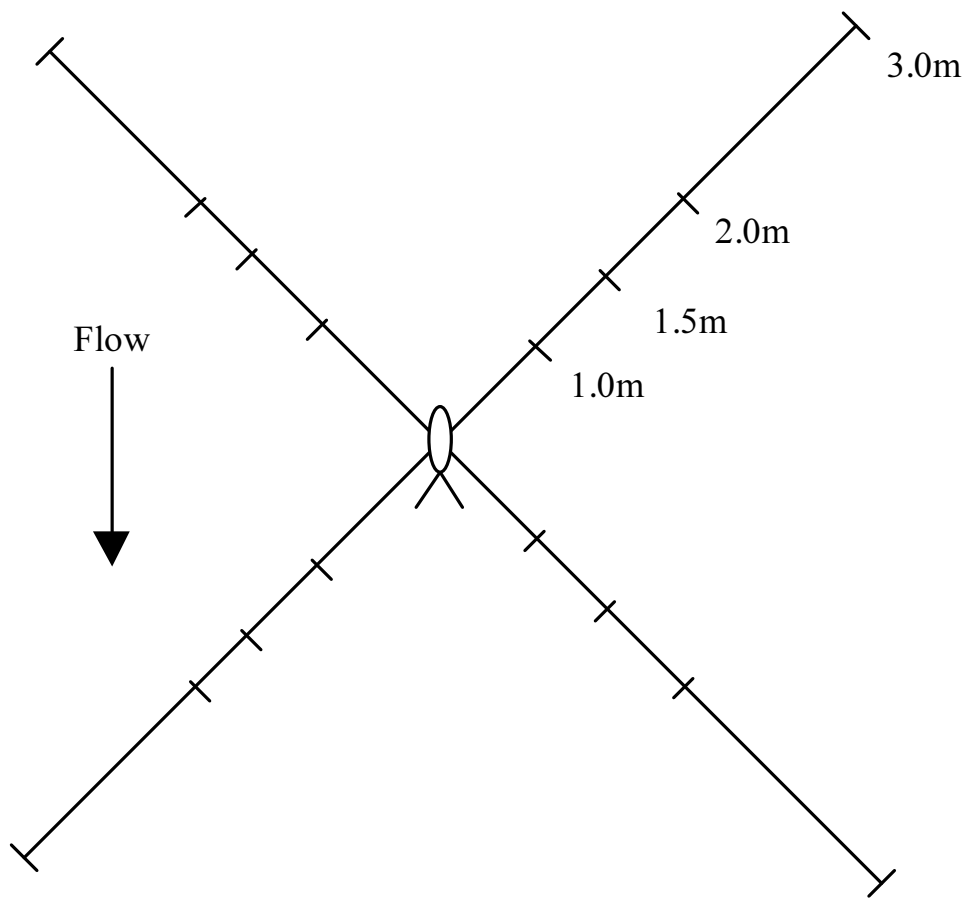
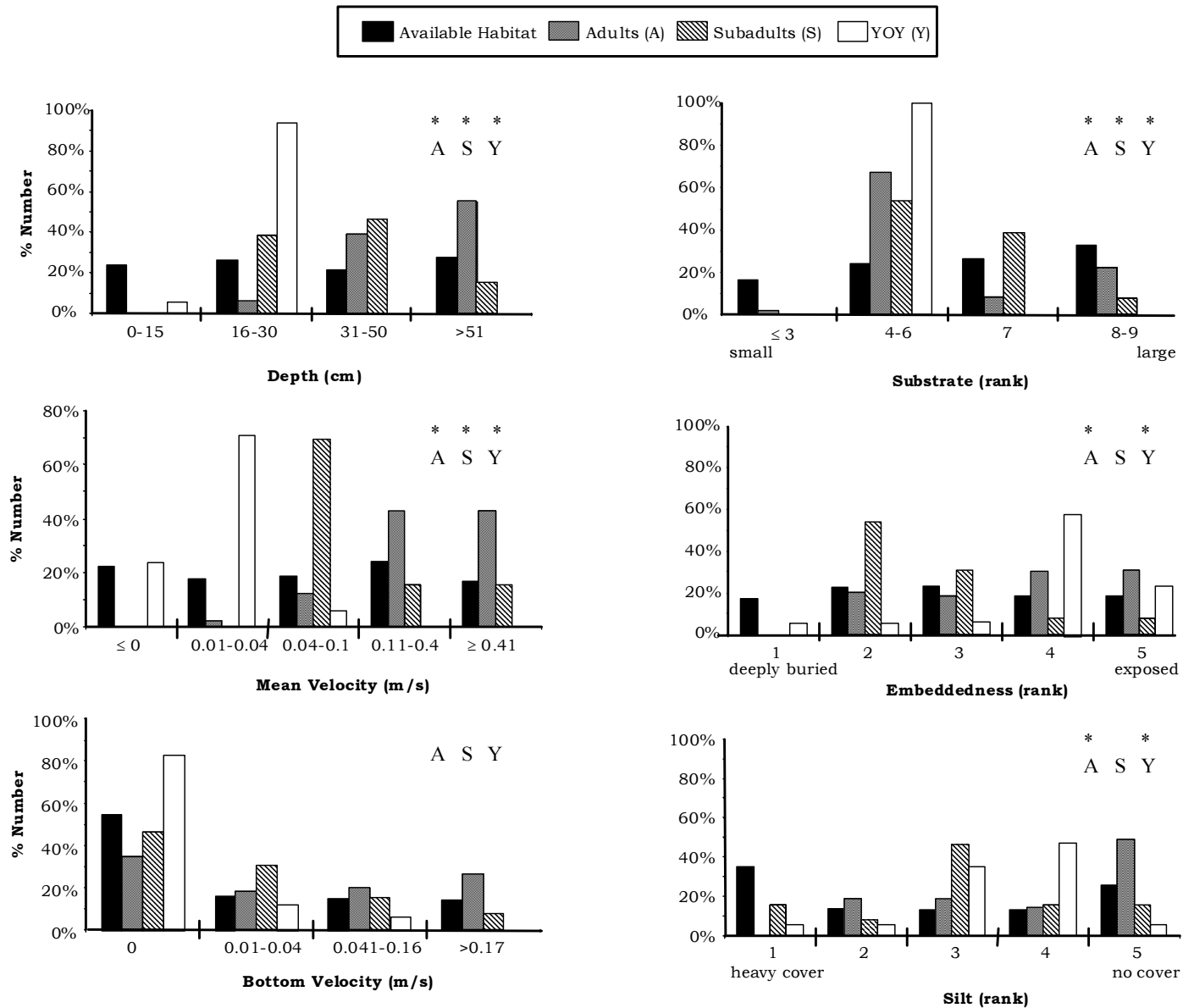


Figure 3.2 Schematic of the “transect cross” technique used to quantify young-of-year habitat use.

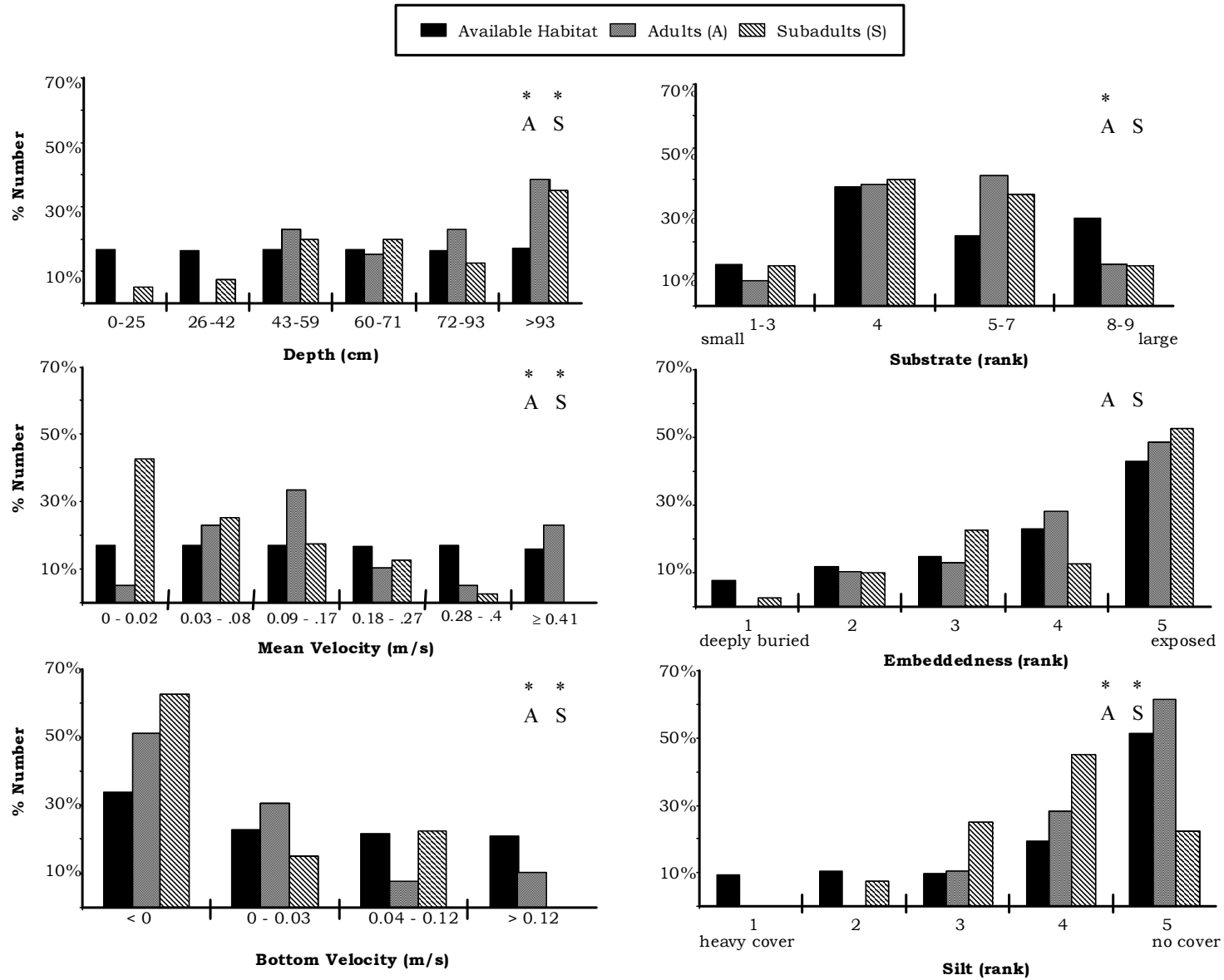
(A)



Roanoke River

Figure 3.3 Proportional abundance of available habitat and proportional occurrence of observed adult, subadult and young-of-year logperch in habitat categories for the Roanoke River (A) and Nottoway River (B), Virginia. * indicates a significant G test at the 0.02 level (Dunn-Sidak correction for multiple tests). Significance indicates non-random selection of a habitat variable by the age class (A = adult, S = subadult, Y = young-of-year).

(B)



Nottoway River

Figure 3.3 (cont)

(A) Roanoke River

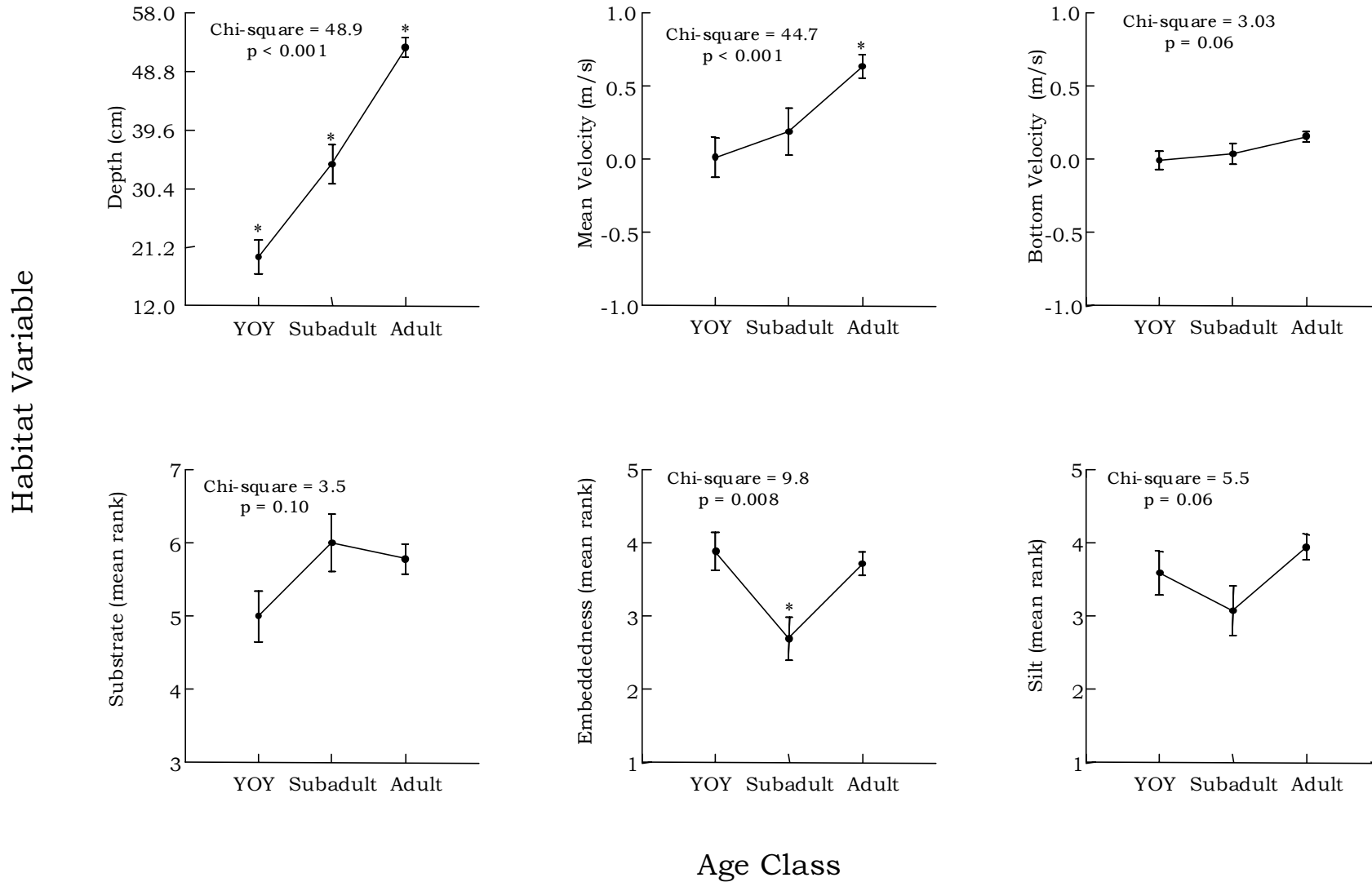


Figure 3.4 Mean habitat use of adult, subadult and young-of-year Roanoke logperch in the Roanoke River (A) and adult and subadult logperch in the Nottoway River (B), Virginia. Error bars indicate 95% confidence interval of the mean. * indicates a significant difference in habitat use (non-parametric multiple comparisons, $\alpha = 0.05$).

(B) Nottoway River

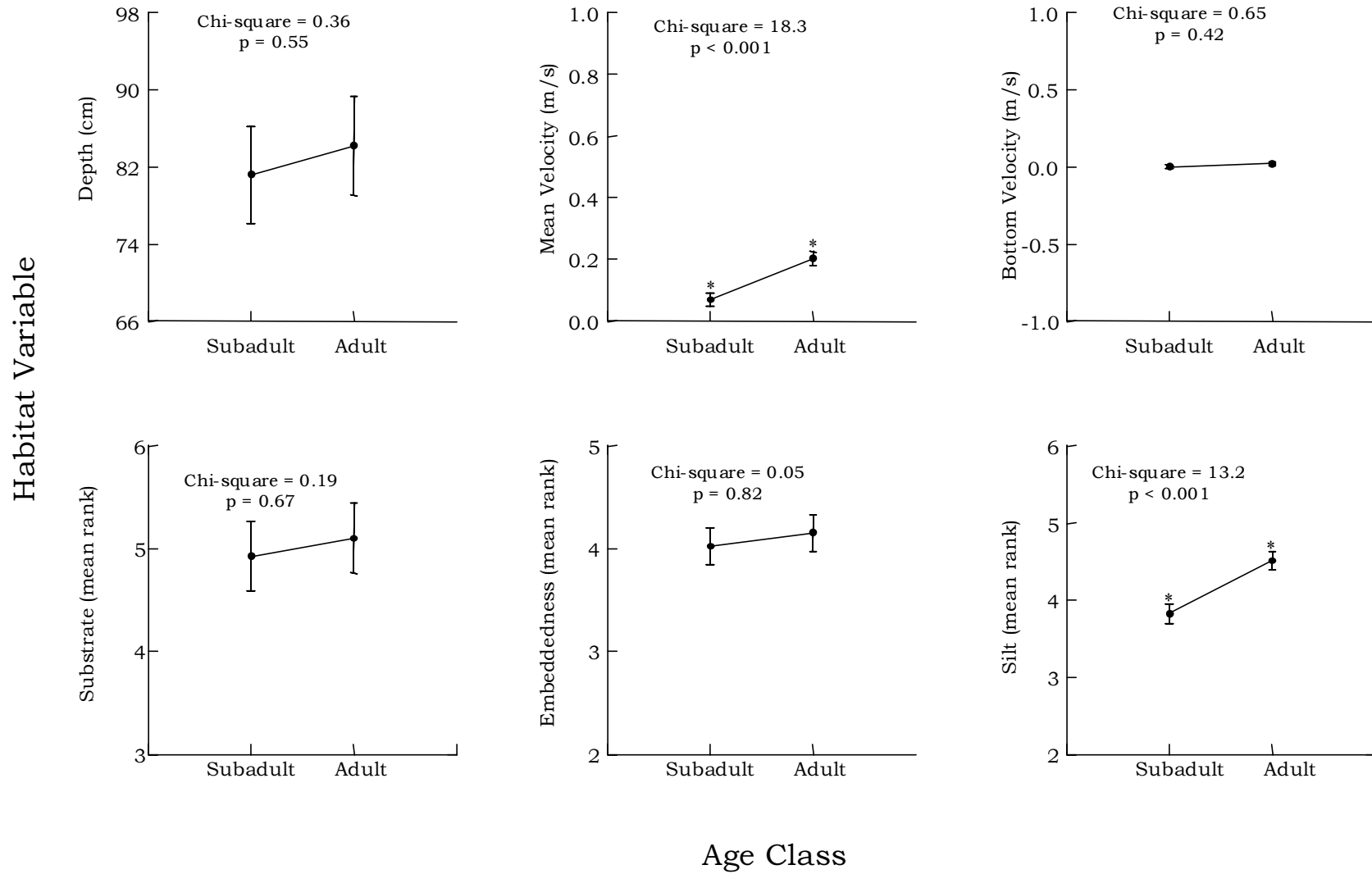


Figure 3.4 (cont)

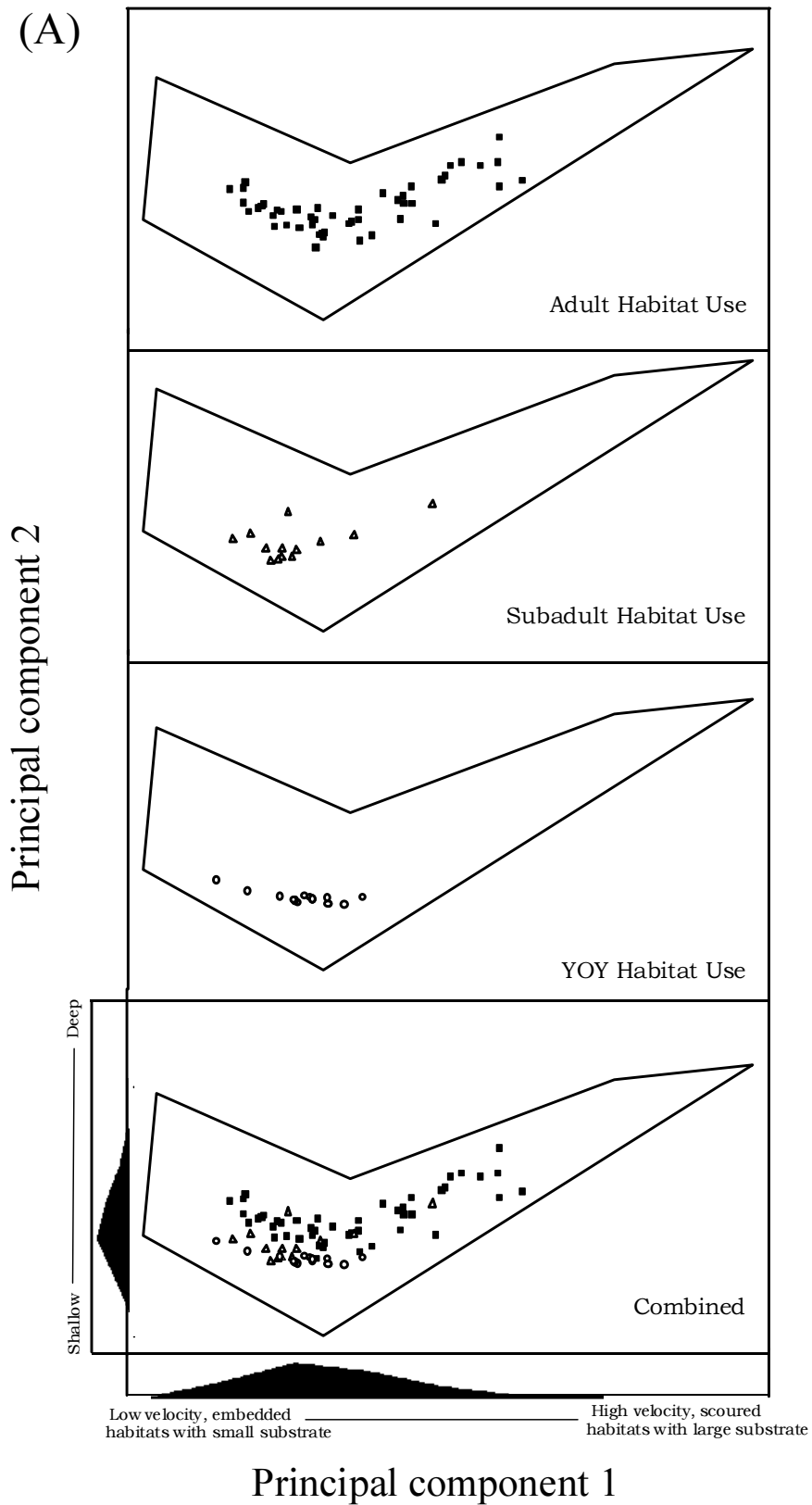


Figure 3.5 A graphic presentation of principal component scores for each age class of Roanoke logperch in the Roanoke River (A) and Nottoway River (B), Virginia. The polygon in each figure circumscribes the area representing available habitat in sampling sites, while the area curves on axes of the bottommost graph represent the relative frequency of

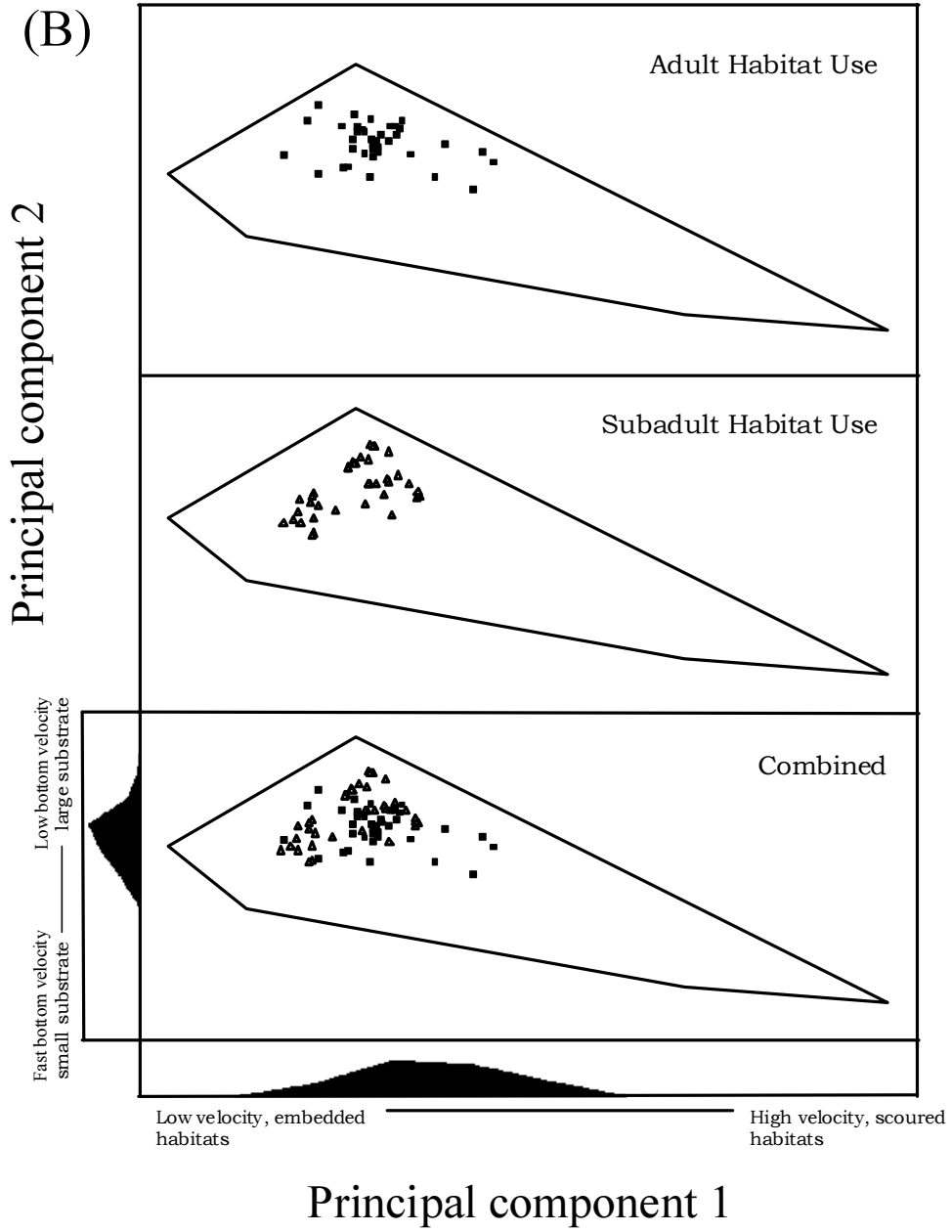


Figure 3.5 (cont)

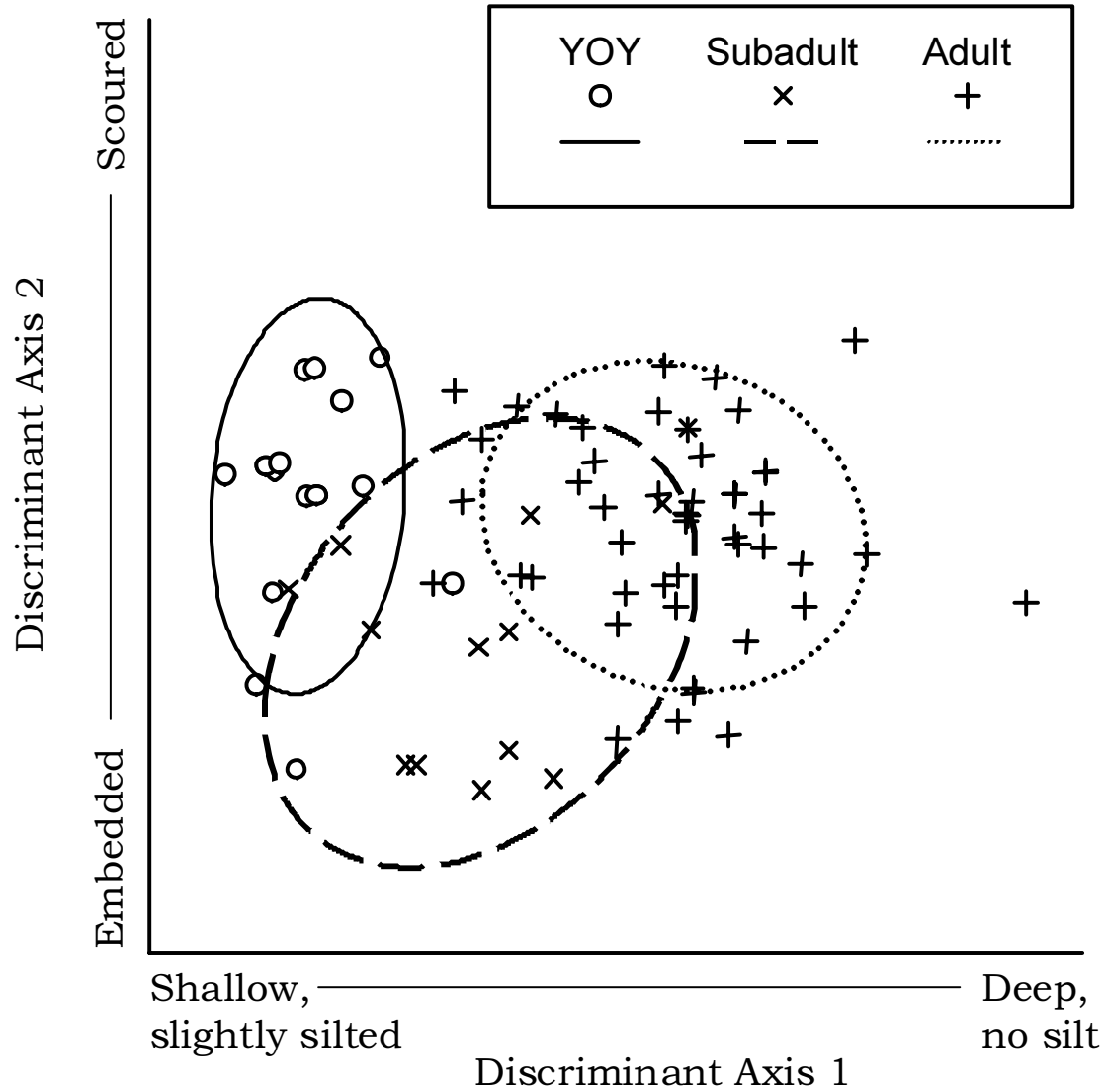


Figure 3.6 Discriminant analysis of habitat use by three age classes of Roanoke logperch in the Roanoke River, Virginia. Ellipses around data points are 95% confidence intervals around mean canonical scores.

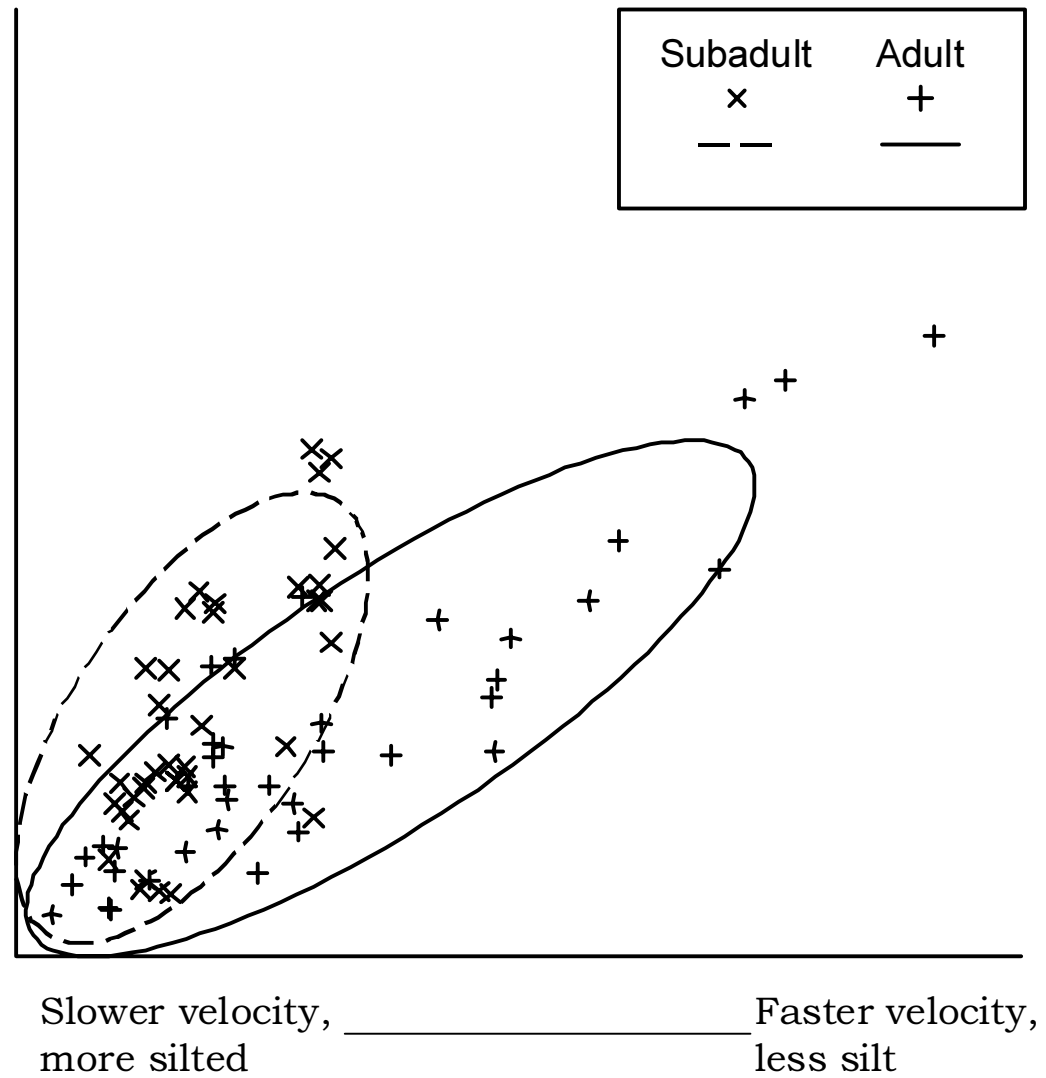


Figure 3.7 Discriminant analysis of habitat use of adult and subadult Roanoke logperch in the Nottoway River, Virginia. Ellipses around data points are 95% confidence intervals around mean canonical scores.

General Conclusions

CONSERVATION OF THE ROANOKE LOGPERCH

I found that each size class of Roanoke logperch clearly and strongly selected particular microhabitat configurations and observed consistency in microhabitat substrate preferences among rivers. Logperch in the Roanoke, Pigg, and Nottoway rivers consistently use silt-free, loosely embedded gravel, probably due to this species' foraging strategy of flipping gravel and small debris to search for small insects. This dissertation suggests that adult logperch, while specializing in microhabitat preferences, are mesohabitat generalists that can occupy a range of velocities and depths to find appropriate substrate for feeding. This specialization indicates that micro-scale conditions are more relevant for Roanoke logperch than meso-scale conditions. However, this species uses a wide range of both micro- and meso-habitats through ontogeny.

Successful conservation of this species will involve the preservation of the ecological processes that maintain required habitat mosaics over multiple scales. Management to enhance populations of Roanoke logperch should focus on enhancement and maintenance of riparian zones and protection of streambanks from agricultural and construction practices that contribute sediment. This type of management is ongoing in the upper Roanoke River; however, efforts will need to be more widespread to enhance slow-water habitats in the Roanoke River and the Pigg River. Management practices in the Nottoway River should focus on prevention of activities that could degrade the high quality habitat available in this system. These practices need to be applied at the watershed scale to achieve micro-scale results. The distribution of habitat types and pathways of dispersal are critical for completion of the logperch life cycle, and habitat heterogeneity at multiple scales will contribute to its continued persistence. Reach-specific management approaches will not ensure the recovery of this species. I instead recommend a watershed-level approach that addresses sediment loading and preserves natural flow regimes that provide ephemeral, seasonal, and persistent types of habitat required over logperch ontogeny.

Future research on the Roanoke logperch should focus on movement related to habitat use among seasons and years and to dispersal pathways that promote population persistence. Further, inventories of habitat types in all river systems will indicate what life stage of the Roanoke logperch is most limited in terms of habitat availability. Additional research should also focus on nesting habitat for Roanoke logperch, a critical life stage not addressed in this dissertation. Genetic studies of Roanoke logperch populations could indicate past bottlenecks, particularly in the Pigg and Smith rivers. In addition, they can indicate the occurrence of evolutionary significant units (e.g., the Nottoway River population) and whether between-river transfers would be an appropriate management action.

BROADER IMPLICATIONS

My study indicates several approaches that may increase the success of habitat studies of an imperiled species that occupies multiple rivers. First, a comparative approach between populations, scales, and life stages can suggest generalized habitat requirements and give insight to what habitat features are most important. Selection of a particular habitat characteristic or a particular habitat scale in one system does not warrant the conclusion that this feature is limiting for the target species. However, if a habitat feature at a certain scale is used consistently regardless of differences in environmental conditions, it is probably important component of the life history of the target species. Creating a mechanistic link between habitat use patterns and the biology of the target species may assist managers in isolating habitat variables important in all rivers within its range. Species like the Roanoke logperch that are sensitive to substrate characteristics at the micro-scale may be less likely to respond to variation between individual mesohabitat units because substrate characteristics do not reliably stratify between pools, riffles, and runs. For the purposes of model transferability, it is clear that the scale at which data are collected should not be chosen arbitrarily. Examination of the strength of habitat selection at different scales offers insight to what scale is most relevant for the species. Finally, this study indicates that species require a habitat mosaic that can

interact over several spatial scales; thus, broader ecological processes that create and maintain this mosaic need to be considered in habitat studies and management plans.

Future studies should address species-specific patterns in habitat model transfer. For example, additional research can examine differences in model transferability in species that are velocity/ depth specialists versus substrate specialists. Habitat models for species that reliably stratify along velocity and depth may be more transferable at the meso-unit scale than the micro-scale. Further, researchers should expand the meso-scale concept. The current paradigm in stream habitat studies is that riffles, runs, and pools are biologically significant, reliable units of stratification at the meso-scale (see Frissel et al. 1986). Identification of these habitat types is based primarily on surface conditions (e.g., turbulence) that may or may not be relevant to stream fishes (Frissel et al. 1986, Vadas and Orth 1998). Other systematic methods to increase grain of observation (e.g., 1 m² to 100 m²) can be used to test if an increase in scale improves model transferability for stream fishes, particularly substrate specialists. Finally, future research on habitat requirements of imperiled stream fishes should encompass on multiple life history stages, pathways of dispersal, and habitat mosaics required over life history. Complete assessment of stream fishes' life history and viability will involve studies that address these key ecological processes and characteristics.

Literature Cited

- Allison, P.D. 1999. Logistic regression using the SAS® System: Theory and application. Cary, NC: SAS Institute, Inc., 304pp.
- Angermeier, P.L. 1985. Spatio-temporal patterns of foraging success for fishes in an Illinois stream. *The American Midland Naturalist* 114:342-359.
- Angermeier, P.L. 1987. Spatiotemporal variation in habitat selection by fishes in small Illinois streams. Pages 52-60 *in* W.J. Matthews and D.C. Heins, editors. *Community and evolutionary ecology of North American stream fishes*. University of Oklahoma Press, Norman.
- Angermeier, P.L. 1992. Predation by rock bass on other stream fishes: experimental effects of depth and cover. *Environmental Biology of Fishes* 34:171-180.
- Angermeier, P.L., K.L. Krueger, and C.A. Dolloff. 2002. Discontinuity in stream-fish distributions: Implications for assessing and predicting species occurrence. Pp. 519-527 *in* J.M. Scott, P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G. Raphael, W.A. Wall, and F.B. Samson, editors. *Predicting species occurrences: issues of accuracy and scale*. Island Press, Covelo, CA
- Angermeier, P.L., and M.R. Winston. 1998. Local vs. regional influences on local diversity in stream fish communities of Virginia. *Ecology* 79:911-927.
- Baltz, D.M., B. Vonderacek, L.R. Brown, and P.B. Moyle. 1987. Influence of temperature on microhabitat choices by fishes in a California stream. *Transactions of the American Fisheries Society* 116:12-20.

- Baras, E. and J. Nindaba. 1999. Diel dynamics of habitat use by riverine young-of-the-year *Barbus barbuis* and *Chondrostoma nasus* (Cyprinidae). *Archiv fur Hydrobiologie* 146: 431-448.
- Bateman, D.S. and H.W. Li. 2001. Nest site selection by reticulate sculpin in two streams of different geologies in the central coast range of Oregon. *Transactions of the American Fisheries Society* 130:823-832.
- Bayley, P.B. and J.T. Peterson. 2001. An approach to estimate probability of presence and richness in fish species. *Transactions of the American Fisheries Society* 130:620-633.
- Belaud, A., P. Chaveroche, P. Lim, and C. Sabaton. 1989. Probability-of-use curves applied to brown trout (*Salmo trutta* Fario L.) in rivers of southern France. *Regulated Rivers Research and Management*. 3:321-336.
- Bell, E., W.G. Duffy, and T.D. Roelofs. 2001. Fidelity and survival of juvenile coho salmon in response to a flood. *Transactions of the American Fisheries Society* 130: 450-458.
- Berkman, H.E. and C.F. Rabeni. 1987. Effect of siltation on stream fish communities. *Environmental Biology of Fishes*. 18: 285-294.
- Beschta, R.L. and W.S. Platts. 1986. Morphological features of small streams: significance and function. *Water Resources Bulletin* 22:369-379.
- Bowlby, J.N. and J.C. Roff. 1986. Trout biomass and habitat relationships in southern Ontario streams. *Transactions of the American Fisheries Society* 115:503-514.
- Bozek, M.A., and F.J. Rahel. 1992. Generality of microhabitat suitability models for young Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) across

- sites and among years in Wyoming streams. *Canadian Journal of Fisheries and Aquatic Sciences*. 49:552-564.
- Breck, J.E., D.L. DeAngelis, W.V. Winkle, and S.W. Christensen. 1988. Potential importance of spatial and temporal heterogeneity in pH, Al, and Ca in allowing survival of a fish population: a model demonstration. *Ecological Modelling* 41:1-16.
- Britton, R.H. and M.E. Moser. 1982. Size-specific predation by herons and its effect on the sex-ratio of natural populations of the mosquito fish *Gambusia affinis* Baird and Girard. *Oecologia(Berl)* 53: 146-151.
- Bult, T.P., R.L. Haedrich, and D.C. Schneider. 1998. New technique describing spatial scaling and habitat selection in riverine habitats. *Regulated Rivers: Research and Management* 14:107-118.
- Burkhead, N.M. 1983. Ecological studies of two potentially threatened fishes (the orangefin madtom, *Noturus gilberti* and the Roanoke logperch, *Percina rex*) endemic to the Roanoke River drainage. Final report to the Wilmington District. U.S. Army Corps of Engineers. Wilmington, NC. 115pp.
- Burkhead, N.M. and H.L. Jelks. 2001. Effects of suspended sediment on the reproductive success of the tricolor shiner, a crevice-spawning minnow. *Transactions of the American Fisheries Society* 130: 959-968.
- Copp, G.H. 1991. Typology of aquatic habitats in Great Ouse, a small regulated lowland river. *Regulated Rivers* 6: 125-134.
- Copp, G.H. 1997. Importance of marinas and off-channel water bodies as refuges for young fishes in a regulated lowland river. *Regulated Rivers: Research and Management* 13: 303-307.

- Copp, G.H., J.M. Oliver, M. Penaz, and A.L. Roux. 1991. Juvenile fishes as functional describers of fluvial ecosystem dynamics: Applications on the River Rhone, France. *Regulated Rivers: Research and Management* 6:135-145.
- Dolloff, C.A., D.G. Hankin, G.H. Reeves. 1993. Basinwide estimation of habitat and fish populations in streams. General Technical Report SE-83. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station 25 pp.
- Dunham, J.B., B.S. Cade, and J.W. Terrell 2002. Influences of spatial and temporal variation on fish-habitat relationships defined by regression quantiles. *Transactions of the American Fisheries Society* 131: 86-98.
- Ensign, W.E., P.L. Angermeier, and C.A. Dolloff. 1995. Use of line transect methods to estimate abundance of benthic stream fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 52:213-222.
- Etnier, D.A. 1997. Jeopardized southeastern freshwater fishes: a search for causes. Chapter four In Aquatic fauna in peril: the southeastern perspective. G.W. Benz and D.E. Collins (editors). Special Publication 1, Southeast Aquatic Research Institute, Lenz Design & Communications, Decatur, Georgia.
- Fausch, K.D. 1983. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Canadian Journal of Zoology* 62:441-451.
- Fausch, K.D. and R.J. White. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. *Canadian Journal of Fisheries and Aquatic Sciences*. 38:1220-1227.

- Flebbe, P.A. 1999. Trout use of woody debris and habitat in Wine Spring Creek, North Carolina. *Forest Ecology and Management* 114:367-376.
- Freeman, M.C., Z.H. Bowen, and J.H. Crance. 1997. Transferability of habitat suitability criteria for fishes in warmwater streams. *North American Journal of Fisheries Management* 17:20-31.
- Frissel, C.A., W.J. Liss, C.E. Warren, and M.D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management* 10:199-214.
- Frost, T.M., D.L. Angelis, S.M. Bartell, D.J. Hall, and S.H. Hurlbert. 1988. Scale in the design and interpretation of aquatic community research in complex interactions. in S.R. Carpenter, editor. *Lake Communities*. Springer Verlag, New York, Inc.
- Gadomski, D.M., C.A. Barfoot, J.M. Bayer, and T.P. Poe. 2001. Early life history of northern pikeminnow in the lower Columbia River Basin. *Transactions of the American Fisheries Society* 130: 250-262.
- Greenberg, L.A. 1988. Interactive segregation between the stream fishes *Etheostoma simoterum* and *E. rufilineatum*. *Oikos* 51: 193-202.
- Groshens, T.P. and D.J. Orth. 1994. Transferability of habitat suitability criteria for smallmouth bass, *Micropterus dolomieu*. *Rivers* 4:194-212.
- Hankin, D.G. and G.H. Reeves. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. *Canadian Journal of Fisheries and Aquatic Sciences*. 45:834-844.
- Hawkins, C.P., J.L. Kershner, P.A. Bisson, M.D. Bryant, L.M. Decker, S.V. Gregory, D.A. McCullough, C.K. Overton, G.H. Reeves, R.J. Steedman, and M.K. Young.

1993. A hierarchical approach to classifying stream habitat features. *Fisheries* 18:3-11.
- Hayes, D.B., C.P. Ferreri, and W.W. Taylor. 1996. Linking fish habitat to their population dynamics. *Canadian Journal of Fisheries and Aquatic Sciences* 53:383-390.
- Hosmer, D.W. and S. Lemeshow 1989. *Applied logistic regression*. Wiley, New York. 307pp.
- Hubert, W.A. and F.J. Rahel. 1989. Relations of physical habitat to abundance of four nongame fishes in high-plains streams: a test of habitat suitability index models. *North American Journal of Fisheries Management* 9:332-340.
- Imhof, J.G., J. Fitzgibbon, and W.K. Annable. 1996. A hierarchical evaluation system for characterizing watershed ecosystems for fish habitat. *Canadian Journal of Fisheries and Aquatic Sciences*. 53:312-326.
- Jenkins, R.E. and N.M. Burkhead. 1993. *Freshwater fishes of Virginia*. American Fisheries Society, Bethesda, Maryland.
- Kynard, B., M. Horgan, and M. Kieffer. 2000. Habitats used by shortnose sturgeon in two Massachusetts rivers with notes on estuarine Atlantic Sturgeon: A hierarchical approach. *Transactions of the American Fisheries Society* 129:487-503.
- Kushlan, J.A. 1976. Wading bird predation in a seasonally fluctuating pond. *Auk* 93:464-476.

- L'Abée Lund, J.H., A. Langeland, B. Jonsson, and O. Ugedal. 1993. Spatial segregation by age and size in Arctic charr: a trade-off between feeding possibility and risk of predation. *Journal of Animal Ecology* 62: 160-168.
- Labbe, T.R. and K.D. Fausch. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. *Ecological Applications* 10:1774-1791.
- Layher, W.G., O.E. Maughan, and W.D. Warde. 1987. Spotted bass suitability related to fish occurrence and biomass and measurements of physicochemical variables. *North American Journal of Fisheries Management* 7:238-251.
- Leftwich, K.N, P.L. Angermeier, and C.A. Dolloff. 1997. Factors influencing behavior and transferability of habitat models for a benthic stream fish. *Transactions of the American Fisheries Society* 126:725-734.
- Leslie, J.K. and C.A. Timmins. 1991. Distribution and abundance of young fish in Chenal Ecarte and Chematogen Channel in the St. Clair River delta, Ontario. *Hydrobiologia* 219:135-142.
- Lohr, S.C. and K.D. Fausch. 1997. Multiscale analysis of natural variability in stream fish assemblages of a western Great Plains watershed. *Copeia* 1997:706-724.
- Mahon, R. and C.B. Portt. 1985. Local size related segregation of fishes in streams. *Archiv fur Hydrobiologie* 103: 267-271.
- Magalhães, M.F. 1993. Effects of season and body size on the distribution and diet of the Iberian Chub *Leuciscus pyrenaicus* in a lowland catchment. *Journal of Fish Biology* 42:875-888.

- Magnan, P. and G.J. Fitzgerald. 1984. Ontogenetic changes in diel activity, food habits and spatial distribution of juvenile and adult creek chub, *Semotilus atromaculatus*. *Environmental Biology of Fishes* 11:301-307.
- Mann, R.H.K. and J.A.B. Bass. 1997. The critical water velocities of larval roach (*Rutilus rutilus*) and dace (*Leuciscus leuciscus*) and implications for river management. *Regulated Rivers: Research and Management* 13:3:295-301.
- Master, L. 1990. The imperiled status of North American aquatic animals. *Biodiversity Network News* 3: 1-2, 7-8.
- Marchetti, M.P. and P.B. Moyle. 2000. Spatial and temporal ecology of native and introduced fish larvae in lower Putah Creek, California. *Environmental Biology of Fishes* 58: 75-87.
- Matthews, W.J. 1985. Critical current speeds and microhabitats of the benthic fishes *Percina roanoka* and *Etheostoma flabellare*. *Environmental Biology of Fishes* 4:303-308.
- McClendon, L.D. and C.F. Rabeni. 1987. Physical and biological variables useful for predicting population characteristics of smallmouth bass and rock bass in an Ozark stream. *North American Journal of Fisheries Management* 7:46-56.
- Meng, L. and S.A. Matern. 2001. Native and introduced larval fishes of Suisun Marsh, California: the effects of freshwater flow. *Transactions of the American Fisheries Society* 130: 750-765.
- Menge, B.A. and A.M. Olson. 1990. Role of scale and environmental factors in regulation of community structure. *TREE* 5:52-57.

- Mérigoux, S. and D. Ponton. 1999. Spatio-temporal distribution of young fish in tributaries of natural and flow-regulated sections of a neotropical river in French Guiana. *Freshwater Biology* 42: 177-198.
- Miller, R.R., J.D. Williams, and J.E. Williams. 1989. Extinctions of North American Fishes during the last century. *Fisheries* 14:22-38.
- Moyle, P.B. and D.M. Baltz. 1985. Microhabitat use by an assemblage of California stream fishes: developing criteria for instream flow determinations. *Transactions of the American Fisheries Society* 114:695-704.
- Olden, J.D. and D.A. Jackson. 2001. Fish-habitat relationships in lakes: gaining predictive and explanatory insight by using artificial neural networks. *Transactions of the American Fisheries Society* 130: 878-897.
- Orth, D.J. 1987. Ecological considerations in the development and application of instream flow- habitat models. *Regulated Rivers: Research and Management* 1:171-181.
- Orth, D.J. and O.E. Maughan. 1982. Evaluation of the incremental methodology for recommending instream flows for fishes. *Transactions of the American Fisheries Society* 111:413-445.
- Orth, D.J. and R.J. White. 1993. Stream habitat management. In C. Kohler and W. Hilbert, editors. *Inland Fisheries Management in North America*. American Fisheries Society, Bethesda, Maryland. pp. 205-230.
- Poff, N.L. 1997. Landscape filters and species traits: towards a mechanistic understanding and prediction in stream ecology. *Journal of North American Benthological Society* 16:391-409.

- Poff, N.L., J.D. Allan, M.B. Bain, J.R. Karr, K.L. Prestegard, B.D. Richter, R.E. Sparks, and J.C. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. *BioScience* 47: 769-781.
- Poizat, G. and D. Pont. 1996. Multi-scale approach to species-habitat relationships: juvenile fish in a large river section. *Freshwater Biology* 36:611-622.
- Power, M.E. 1984. Depth distributions of armored catfish: predator induced resource-avoidance? *Ecology* 1984:523-528.
- Power, M.E. 1987. Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size. Pp 333-353 In Predation: direct and indirect impacts on aquatic communities. Kerfoot, W.C. and Sih, A., (editors). Hanover: University press of New England.
- Rabeni, C.F. and S.P. Sowa. 1996. Integrating biological realism into habitat restoration and conservation strategies for small streams. *Canadian Journal of Fisheries and Aquatic Sciences* 53(Supplement 1):252-259.
- Reice, S.R., R.C. Wissmar, and R.J. Naiman. 1990. Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. *Environmental Management* 14:647-659.
- Richter, B.D., D.P. Braun, M.A. Mendelson, and L.L. Master. 1997. Threats to imperiled freshwater fauna. *Conservation Biology* 11:1081-1093.
- Rosenberger, A.E. and P.L. Angermeier. 2002. Roanoke Logperch (*Percina rex*) Population Structure and Habitat Use. Final Report submitted to the Virginia Department of Game and Inland Fisheries, Blacksburg, VA. 110pp.

- Ruzycki, J.R. and W.A. Wurtzbaugh. 1999. Ontogenetic habitat shifts of juvenile Bear Lake sculpin. *Transactions of the American Fisheries Society* 128: 1201-1212.
- Scheidegger, K.J. and M.B. Bain. 1995. Larval fish distribution and microhabitat use in free-flowing regulated rivers. *Copeia* 1995: 125-135.
- Schlosser, I.J. 1987. The role of predation in age- and size- related habitat use by stream fishes. *Ecology* 68:651-659.
- Schlosser, I.J. 1988. Predation risk and habitat selection by two size classes of a stream cyprinid: experimental test of a hypothesis. *Oikos* 52:36-40.
- Schlosser, I.J. and P.A. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. *American Fisheries Society Symposium* 17:392-401.
- Schlosser, I.J. and L.A. Toth. 1984. Niche relationships and population ecology of rainbow (*Etheostoma caeruleum*) and fantail (*E. flabellare*) darters in a temporally variable environment. *Oikos* 42:229-238.
- Tonn, W.M., J. J. Magnuson, M. Rask, and J. Toivonen. 1990. Intercontinental comparison of small-lake fish assemblages: the balance between local and regional processes. *The American Naturalist* 136: 345-369.
- Tramer, E.J. 1977. Catastrophic mortality of stream fishes trapped in shrinking pools. *American Midland Naturalist* 97:469-478.
- Vadas, R.L. and D.J. Orth. 1998. Use of physical habitat variables to discriminate visually determined mesohabitat types in North American streams. *Rivers* 6:143-159.

- Vadas, R.L. and D.J. Orth. 2000. Habitat use of fish communities in a Virginia stream system. *Environmental Biology of Fishes* 59:253-269.
- Watson, G. and T.W. Hillman. 1997. Factors affecting the distribution and abundance of bull trout: an investigation at hierarchical scales. *North American Journal of Fisheries Management* 17:237-252.
- Welsh, S.A. and S.A. Perry. 1998. Influence of spatial scale on estimates of substrate use by benthic darters. *North American Journal of Fisheries Management* 18:954-959.
- Werner, E.E. and J. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual review of ecology and systematics* 15:393-425.
- Werner, E.E. and D.J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology* 69:5:1352-1366.
- Wiens, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.
- Williams, D.E. 1976. Improved likelihood ratio tests for complete contingency tables. *Biometrika* 63:33-37.
- Williams, J.E., J.E. Johnson, D.A. Hendrickson, S. Contreras-Balderas, J.D. Williams, M. Navarro-Mendoza, D.E. McAllister, and J.E. Deacon. 1989. Fishes of North America endangered, threatened, or of special concern: 1989. *Fisheries* 14:2-3.
- Williams, J.E., M.L. Warren, Jr., K.S. Cummings, J.L. Harris, and R.J. Neves. 1993. Conservation status of freshwater mussels of the United States and Canada. *Fisheries* 18:6-22.

Williams J.E., C.A. Wood, and M.P. Dombeck, editors. 1997. Watershed restoration: principles and practices. American Fisheries Society, Bethesda, Maryland.

Appendix A. Composite model of logperch habitat use.

INTRODUCTION

The focus of the first two chapters of this dissertation is the transferability of multiscale models of logperch habitat use among locations. The theoretical focus of these chapters precluded the development of a model that would work best for the purposes of the management of Roanoke logperch. The purpose of this appendix is to present a composite, generalized model that best fits the patterns of logperch habitat use I observed in the Roanoke, Pigg, and Nottoway rivers. The overall fit and transferability of this model will be presented in comparison to the fit and transferability of individual models presented in Chapter I. Because the previous chapters focus on model transfer, models presented in these chapters were created as if I did not have any knowledge of habitat use in other systems. This model is created with knowledge from all systems and therefore will be more useful for general application.

METHODS

Methods for data collection are presented in Chapters 1 and 2. I developed a logistic regression model based on all of the data combined for each river relating habitat variables to the presence of logperch (SAS® System Version 8.2, Cary, NC). River of origin is used as a class variable (1 = Roanoke, 2 = Nottoway, 3 = Pigg). To obtain the most parsimonious models possible, variables used in the logistic regression, including interaction terms, were eliminated from the model using backwards selection. Variables typically were eliminated because they strongly covaried with other habitat variables or did not significantly contribute to the fit of data to the model (no or slight increase in AIC criterion or a non-significant Wald χ^2). Multicollinearity assumptions were met for this model. I verified the fit of the composite model by evaluating the ability of the model to predict the presence of logperch (sensitivity) from available habitat (specificity) in the data set from which the model was developed. I used a cutoff value equal to the proportion of presences and availability for all rivers combined

(0.047). The performance of the composite model was compared to performance of the individual microhabitat models presented in Chapter one using sensitivity, specificity and AIC measures.

RESULTS

The composite model, like the models based on data sets from the individual rivers (see Chapter 1), showed a nonrandom distribution of Roanoke logperch over available habitat configurations ($\chi^2 = 90.6$, $P < 0.0001$, Table A.1). This model indicated that logperch were most likely to be observed in the Roanoke and Nottoway rivers and were positively associated with depth and water velocity and negatively associated with silt cover (Table A.1). In addition, depending on water velocity, logperch preferred larger dominant substrates.

The sensitivity and specificity of the composite model on the combined data set was well balanced (0.70/0.70) compared to the sensitivity and specificity of self-verified models (Table A.2). In addition, the AIC criterion from each model indicates that the composite model fits the individual data sets better than the single river models, with the exception of the Roanoke River model when applied to the Roanoke River data set. However, the AIC criterion from the composite model when applied to the Roanoke River data set is comparable to the AIC criterion from the Roanoke River model.

DISCUSSION

The significance, fit, and balanced accuracy of the composite model indicates that it is the best model overall to apply to identify areas suitable for Roanoke logperch. Variables important in the individual models (Table 1.6) were also important in the composite model. Potential uses of the overall model include identification of suitable areas for reintroduction and of new areas likely to contain logperch within its distributional range.

Table A.1 Logistic regression model used to estimate probability of presence of Roanoke logperch in microhabitat locations in the Roanoke, Pigg, and Nottoway rivers, Virginia. Parameter estimates are maximum-likelihood estimates, and the significance of each variable is based on Wald χ^2 . Significance of each model is based on a χ^2 of the $-2 \log$ -likelihood statistic. River 1 = Roanoke River; River 2 = Nottoway River; Pigg River = 3 class terms.

Composite Model		($\chi^2 = 90.6$, df = 5, P < 0.0001)		
Variable	Parameter Estimate	χ^2	df	P
Intercept	-7.75	113.9	1	< 0.0001
River 1	0.34	4.7	1	0.03
River 2	-1.03	27.1	1	< 0.001
Depth (cm)	0.02	32.4	1	< 0.001
Mean velocity (m/s)	2.94	7.4	1	0.007
Dominant substrate (rank)	0.25	11.6	1	0.0007
Silt (rank)	0.53	23.6	1	< 0.0001
Average velocity x Dominant substrate	-0.35	6.2	1	0.013

Table A.2 Characteristics of logistic regression models developed to predict the presence of Roanoke logperch in the Roanoke, Pigg, and Nottoway rivers, Virginia. The relative performance of each model is presented using sensitivity/ specificity and AIC criterion. Models presented include models based on data from individual rivers (see Chapter I) and the data set from all rivers combined. Underlined values indicate self-verification.

Data Source for logistic regression models

Sensitivity/ Specificity

Roanoke River	Pigg River	Nottoway River	All rivers combined
<u>0.93/ 0.43</u>	<u>0.64/ 0.79</u>	<u>0.57/ 0.80</u>	<u>0.70/0.70</u>

Data Source for logistic regression models

Models transferred to:	AIC			
	Roanoke River	Pigg River	Nottoway River	All rivers combined
Roanoke River data sets	<u>363.5</u>	373.0	370.1	364.6
Pigg River data sets	108.6	<u>111.6</u>	104.8	106.9
Nottoway River data sets	251.6	250.7	<u>275.4</u>	249.7

Appendix B. Observations of seasonal habitat use by Roanoke logperch.

INTRODUCTION

Seasonal habitat use by Roanoke logperch is one of the major gaps in our knowledge of this species' habitat use and life history. My objective in this study is to compare habitat use by logperch between summer and winter. This basic information will contribute to effective recovery efforts and will enhance managers' understanding of factors that limit logperch distribution and abundance relevant to the long-term viability of logperch populations.

METHODS

In the summer of 1999, a reachwide inventory of 10 km of the Roanoke River was conducted using the Basinwide Visual Estimation Technique described in Dolloff et al. (1993). Eight riffle:run:pool series were systematically selected from these reachwide inventories for summer quantitative underwater observation using line transect snorkeling methods. Winter protocols for sampling in the Roanoke River included strip transect methods outlined in Ensign et al. (1999). This method met with limited success in 1998-1999. New methods were used in the Roanoke River for the winters of 1999 and 2000.

Summer survey observations for each riffle:run:pool series were made via line-transect snorkeling methods described in Ensign et al. (1995) and in Chapters 1 and 2. Sampling methods for the winters of 1998-1999 in the Roanoke River followed methods outlined by Ensign et al. (1999). Previous work indicated that logperch are quiescent in winter, residing in interstitial spaces between boulders and cobbles (Burkhead 1983, Ensign et al. 1999). To sample for logperch, a team of three divers swam along a 50-m longitudinal transect along the deepest part of the channel and along 10-m perpendicular transects centered at the 5-, 15-, 25-, 35-, and 45-m locations on the longitudinal transect. One of the divers turned over cobbles and boulders within a 15-cm wide strip along these transects to search for logperch, while the other divers flanked the first diver, recorded data on dive slates, and set underwater markers where logperch were observed. For each site, attempts were made to sample a riffle and pool. Habitat availability was measured at 5-m intervals along the 45-m transect and the five perpendicular

transects. Habitat data included depth, mean and bottom velocities, substrate size (5-category Wentworth scale), and silt cover. This sampling protocol was time-intensive; each transect line took about 7 hours to census completely and covered only 13.5 m² of the stream bottom.

Limited success in the winters of 1998 and 1999 led to the development of alternative winter sampling methods for Roanoke logperch. These methods allowed the sampling of a greater variety of habitat types, and, unlike the strip transect method, did not restrict divers to the thalweg of the river. It also allowed all three divers to search for logperch, rather than a single diver. A team of three snorkelers moved up a previously delineated riffle, run, pool sequence in a zigzag fashion, turning all lightly embedded cobbles, boulders, and deadfall substrate in a shoulder-wide (~50cm) strip to count logperch. Divers concentrated on sampling a variety of habitats. When a logperch was observed, a weighted marker was placed at the site of observation. After the selected river length was sampled, divers returned to these sites to take sighting location and habitat data. In one day, three snorkelers would typically sample an entire riffle, run, pool sequence (~100 m long), with a total of ~150 m² of the stream bottom intensively searched.

At each location where a logperch was observed, the following information was recorded: distance of sighting from stream bank (left or right), description of rock formation, and mesohabitat type. Habitat use and availability data were recorded at the site where each fish was observed using a cross-shaped transect, which was centered on the logperch sighting location (Figure 1). Habitat use data were taken along transect arms set at 45°, 135°, 225°, and 315° from this center sighting location (Figure 1). These angles minimized collection of habitat data in areas where divers had disturbed substrate. Habitat use was measured at five points, including the site of observation and 0.25 m from the center point along each transect line (four 0.25-m measurements). Habitat availability was measured at 16 points, including 1, 1.5, 2.0, and 3.0 m from the center point along each transect. The following habitat variables were recorded at each point: depth, mean water velocity, bottom water velocity (if possible, measured behind rock where logperch was sighted), rank embeddedness, and rank substrate size.

Data analysis

We made 6 attempts to observe Roanoke logperch in the Roanoke River during winter, and sampled 8 sites in the Roanoke River during summer (Table B.1). Due to the limited

window of opportunity and area sampled, only 5 adult Roanoke logperch were observed during winter months from 1999-2000. Microhabitat data that were comparable using summer and winter methods included depth (cm), mean velocity (m/s), bottom velocity (m/s), point substrate (rank category), embeddedness (rank category), and silt cover (rank category). Differences between winter and summer habitat use for each characteristic was tested with Mann-Whitney U tests.

RESULTS

Logperch observed in the summer were found in deep, high velocity microhabitats with exposed, silt-free gravel substrate. Logperch observed in winter months selected deep microhabitats around exposed gravel and cobble substrate. We could not detect differences between seasons in logperch use of substrate or water depths ($\chi^2 < 0.99$, $P > 0.32$, Table B.2). However, logperch observed in the winter appeared to use habitat with slower mean and bottom water velocities than logperch observed in summer months ($\chi^2 > 7.3$, $P < 0.008$, Table B.2). In addition, logperch in the winter were observed in less embedded substrate than logperch observed in the summer ($\chi^2 = 6.9$, $P = 0.008$, Table B.2). Logperch in the winter also appeared to select less silted habitat than logperch in the summer, though the Mann-Whitney U test was only marginally significant ($\chi^2 = 3.6$, $P = 0.06$, Table B.2).

DISCUSSION

Prior to this study, it has been proposed that logperch use deep pools for winter habitat (Burkhead 1983). Our limited observations suggest that this is not so; winter habitat use of Roanoke logperch is not as dramatically different from summer habitat use as has been suggested. Adults observed in both seasons were found in high-velocity, deep microhabitat in riffles and runs over exposed, silt-free gravel in areas dominated by cobble and boulder substrate. However, even with our low sample size, we were able to detect some key seasonal differences in logperch habitat use. Logperch in the winter appeared to use lower water velocities than logperch in the summer. Swimming ability of logperch in the winter may be limited due to cold temperatures that depress metabolism. Use of lower bottom velocities would reduce necessary

activity for quiescent individuals. In addition, logperch observed in the winter were found over substrate that was less embedded with smaller substrates and less covered with silt. Because logperch require interstitial pockets within cobbles and boulders for resting in the winter, it is not surprising that logperch use particularly silt-free, unembedded substrate. It is possible that logperch are even more specialized in substrate preferences in the winter than the summer. For active logperch during summer months, some embeddedness and silt cover may not be a significant deterrent.

Table B.1 Summary of sites visited in the Roanoke River during summer and winter months, including water quality information (per site), number of Roanoke logperch observed, and mesohabitat types sampled.

Season	# sites	mesohabitats	observations (mean, SD)	DO (mg/L, mean, SD)	Temp (°C, mean, SD)	Cond (µs, mean, SD)
Summer	8	pool, riffle, run	6.14 ± 9.8	9.6 ± 1.3	20.5 ± 2.4	346.4 ± 29.1
Winter	5	pool, riffle, run, secondary channel	1 ± 0.7	14.2 ± 0.6	5.8 ± 2.8	382.9 ± 3.1

Table B.2 A comparison of summer and winter habitat use by Roanoke logperch in the Roanoke River based on surveys conducted from 1999-2001. ** Indicates a significant difference at the 0.05 level (Mann-Whitney U-test); * Indicates marginal significance.

Habitat variable	Summer	Winter	χ^2	P	
Depth (cm), SD	51.5 ± 12.8	66.0 ± 29.1	0.99	0.32	
Mean velocity (m/s), SD	0.59 ± 0.68	0.46 ± 0.21	12.2	< 0.001	**
Bottom velocity (m/s), SD	0.15 ± 0.30	0.03 ± 0.04	7.34	0.007	**
Substrate (mean rank), SD	5.8 ± 1.6	6.2 ± 1.1	0.58	0.47	
Embeddedness (mean rank), SD	3.8 ± 1.1	5.0 ± 0.0	6.9	0.008	**
Silt Cover (mean rank), SD	4.0 ± 1.2	5.0 ± 0.0	3.6	0.06	*
N	54	5			

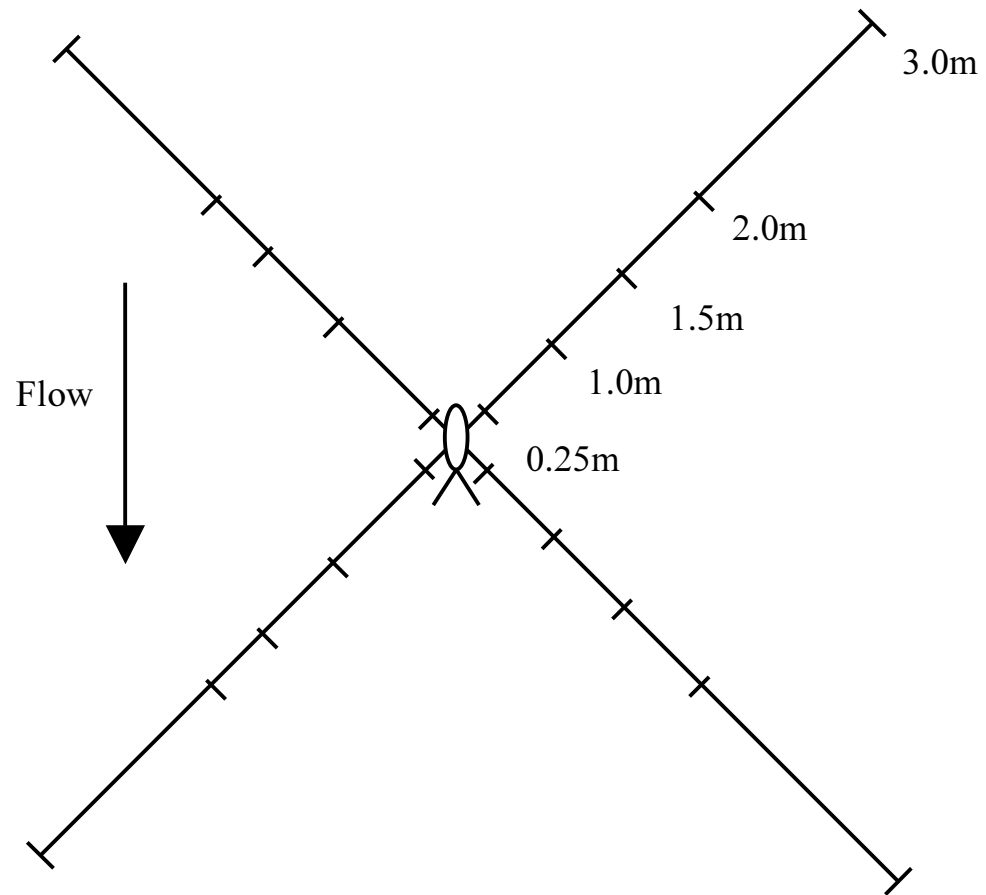


Figure B.1 Schematic of “transect cross” used to sample habitat during winters of 1999-2000. This transect was also used to quantify habitat use of YOY logperch (see Chapter 3).

Vita

Amanda Rosenberger was born in Richmond, Virginia on 14 August 1974. From the age of 2 until the age of 16, she lived in Newport News, Virginia. She developed a strong interest in aquatic environments while sailing and canoeing in the Chesapeake Bay watershed. Her parents cultivated her interest in the biological sciences by taking her to museums and zoos as well as snorkeling vacations in the Caribbean. Encouraged by her parents and grandmother, she also developed a keen interest in paleontology. Dissatisfied with the curriculum of her local high school, she left at the age of 16 to attend Simon's Rock College of Bard in Great Barrington, Massachusetts. She has yet to earn a high school diploma.

At Simon's Rock College, Amanda met her first mentor and inspiration, Bob Schmidt, who introduced her to the biological sciences and aquatic fieldwork. Bob and his colleague, Don Roeder, took Amanda out on field trips for class and employed her as a volunteer and paid assistant for their research projects. Dr. Schmidt also developed a field course in Guyana and organized field trips in 1993 and 1994. Attending these field trips inspired Amanda to pursue graduate studies in tropical ecology. Amanda earned her Associate degree at Simon's Rock College in 1992 and her Bachelor of Arts degree in 1994.

Amanda received a Master of Science degree in 1997 from the University of Florida, where she worked in the Department of Zoology under the supervision of Dr. Lauren Chapman. Her studies focused on the potential of wetland habitats near Lake Victoria, East Africa, as refugia for native fishes endangered by the introduction of a non-native predator, Nile perch. The Lake Victoria fauna was once considered the most diverse in the world until the introduction of the Nile perch eradicated over 300 native species found in the lake. She and Lauren Chapman's research team found that wetland habitats may be critical habitat for a large subset of the remnant Lake Victoria fauna, and these habitats may seed resurgence and restoration of the native community. Components of her Master's work have been published in the Ecology of Freshwater Fishes and the Journal of Fish Biology. Amanda's academic and professional skills thrived under the mentorship and guidance of Lauren Chapman. While at the University

of Florida, Amanda met the love of her life, Till Rosenberger. She married him in May of 1997.

Together Amanda and Till moved to Blacksburg, Virginia, where she could pursue her interest in aquatic ecology with Dr. Paul Angermeier. Amanda owes all of her academic success to her mentors, friends, and family. Now she has additional inspiration in the form of her lovely daughter, Nora Bailie Rosenberger, who was born September 11, 2002. She will travel to Boise, Idaho with her family to pursue postdoctoral studies at the Forest Service Rocky Mountain Research Station.