

Multiple-Scale Habitat Models of Benthic

Fish Abundance in Riffles

by

William E. Ensign

Dissertation submitted to the Faculty of the

Virginia Polytechnic Institute and State University


in partial fulfillment of the requirements for the degree of


DOCTOR OF PHILOSOPHY

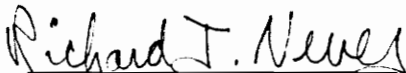
IN

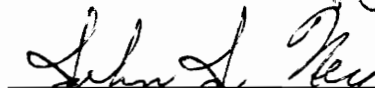
FISHERIES AND WILDLIFE SCIENCES

APPROVED:


Paul L. Angermeier, Co-Chair


C. Andrew Dolloff, Co-Chair


Richard J. Neves


John J. Ney


Jackson R. Webster

August, 1995

Blacksburg, Virginia

Keywords: Stream Fish, Habitat, Abundance, Spatial Scale, Visual Estimation

C.2

LD

5655

V856

1995

E 575

C.2

**Multiple-scale habitat models of benthic fish
abundance in riffles**

by

William E. Ensign

Committee Co-Chairs: Paul L. Angermeier and C. Andrew Dolloff

ABSTRACT

This dissertation examines the relationship between abundances of Roanoke darter, Roanoke logperch, and black jumprock and availability of stream habitat features at three spatial scales in two reaches of the Roanoke River, Virginia. The utility of underwater observation as a method of estimating benthic fish densities is also assessed. Distributions of perpendicular sighting distances indicate models assuming equal sighting probability are not appropriate for benthic species but distance sampling models assuming decreased sighting probability with increased distance from observers provide reasonable alternatives. Abundances estimated using two distance sampling models, a strip transect model, and a backpack electroshocker were strongly correlated.

At the microhabitat scale (45 m² cells), differential use of depth, velocity, substrate, and siltation level by all three species during summer low flows was evident. Habitat use characteristics were not transferable, as depths and velocities associated with high fish densities varied between reaches. Univariate and multivariate habitat suitability indices gave similar rankings for combinations of the four habitat variables, but site suitabilities based on these indices were poor predictors of fish abundance. Habitat cells were not selected independently of surrounding habitat characteristics, as fish densities were highest in target cells adjacent to cells with preferred microhabitat characteristics. Roanoke darter and black jumprock abundances were highest at sites where preferred microhabitat patches were non-contiguous while contiguity had no effect on logperch abundance. Multiple regressions showed area of suitable habitat and patch contiguity accounted

for 42%, 34%, and 33% of variation in darter, logperch, and jumprock abundances, respectively. Estimates of area of target riffles, area of pools and riffles upstream and downstream of target riffles, and depth, velocity, and substrate characteristics of pools and riffles immediately upstream and downstream of target riffles were obtained. Fish densities were correlated with at least one measure of proximal habitat for all three species. Significant multiple regression models relating fish density to adjacent habitat unit characteristics were also obtained, but the explanatory power of adjacent unit variables varied among small, medium and large riffles and among species. In summary, fish abundance was related to habitat at all spatial scales but explanatory power was limited.

Acknowledgements

Although the mistakes, misinterpretations, and errors in this dissertation are attributable solely to me, the good things to be found in the following pages resulted from the contributions of numerous people. The funding that allowed me to do field work, hire technicians, analyze data, and put an occasional meal on the table was provided by the Department of Fisheries and Wildlife at Virginia Tech, the Wilmington District of the U. S. Army Corps of Engineers, the Virginia Department of Games and Inland Fisheries, and the U. S. Fish and Wildlife Service. Rather than directing me down a path of their own choosing, my committee co-chairs, Paul Angermeier and Andy Dolloff, allowed me the freedom to pursue non-traditional approaches to the relationships between stream fish and the places they live. They also had the wisdom to pull me back when I ventured onto ice too thin to support the weight of my ideas. I appreciate both the carrot and the stick they wielded over the past few years. The other members of my committee, John Ney, Dick Neves, and Jack Webster, were always willing to offer advice, suggestions, and constructive criticism when given the opportunity. Don Orth and Dean Stauffer served as unofficial committee members, lending an empty office chair and a willing ear when quizzed about the intricacies of habitat modeling approaches. My academic progress has been fostered by a number of outstanding educators, including the entire staff of Missionary Ridge Elementary School in Chattanooga, Tennessee, Henry Merchant at George Washington University, and Dewey Bunting, Dave Etnier, and Richard Strange at the University of Tennessee.

One of the advantages of residing in a large academic department comes from the wealth of alternative views (some good, some not so good) generated by fellow graduate students. In this regard, Matt Sabo, Ed Pert, Heather Pert, Bob Vadas, John Morton, Mike Tonkovich, Dave Hewitt, Steve McMullin, Alan Temple, Martin O'Connell, John Loegering, Eric Schradling, and Roy Smogor

always provided interesting thought food and healthy critiques of the meager mental meals I offered. Although the final product of the pursuit of the doctoral degree is this pile of paper called a dissertation, the data presented represent many hours of sweat, suffering, and plain hard work by a group of very capable field technicians. Ryan Barnes, Maya Khosla, Roberta Swift, Caroline Wiecking, Pat Lookabaugh, and Marty Underwood put up with cold water, hot days, piles of fish, unidentified objects in the Roanoke River, winos in Wasena Park, cattle in the South Fork Roanoke, and innumerable other miseries. Kevin Leftwich deserves special recognition for his multiple roles as technician, fellow graduate student, turf management and swing dynamics advisor, provider of tasty venison, and most importantly, valued friend.

I want to thank my parents, Bill and Elaine Ensign, as they provided emotional, intellectual, and financial support as well as fostering the sense of wonder and curiosity about the world that has allowed me to live a rich and full life to this point. Finally and most of all, I wish to thank my wife, Renee Speenburgh. She has cheerfully supported me, both emotionally and financially, during the course of my graduate work. Ten years ago, Renee agreed to two shaky propositions, marriage to me and my pursuit of graduate degrees. Happily, the latter has come to an end and hopefully, the former never will.

TABLE OF CONTENTS

INTRODUCTION TO THE DISSERTATION	1
Study Area	6
Study Species	11
 CHAPTER 1: Use of Line Transect Methods to Estimate Abundance of benthic stream fishes	 13
Introduction	13
Methods	14
Study area and study species	14
Underwater observation	16
Electrofishing	18
Density estimation	19
Statistical analysis	23
Results	23
Sighting distances	23
Estimator comparisons	26
Discussion	32
Adequacy of the strip transect sighting model	32
Adequacy of line transect models	35
Comparisons among estimates	37
Conclusions	38
 CHAPTER 2: Microhabitat Suitability as an Indicator of Benthic Fish Abundance in Riffles	 41
Introduction	41
Methods	43
Study area	43
Microhabitat use quantification	45
Abundance estimation	47
Development of measures of habitat use	47
Statistical analysis	50
Results	54
Habitat use	54
Comparison of suitability indices	62
Abundance-weighted usable area correlations	66
Discussion	68
Habitat use	68

Comparison of suitability indices	71
Microhabitat availability/abundance correlations	72
CHAPTER 3: Intermediate-Scale Measures of Habitat as Predictors of Benthic Fish Abundance in Riffles	80
Introduction	80
Methods	83
Field data collections	83
Importance of adjacent cell habitat	83
Combined microhabitat-adjacent cell suitability site ratings	84
Spatial distribution of suitable habitat	85
Combined models	87
Results	88
Importance of adjacent cell habitat	88
Combined microhabitat-adjacent cell suitability site ratings	92
Spatial distribution of suitable habitat	92
Combined models	101
Discussion	105
Adjacent cell suitability	105
Spatial distribution of suitable habitat	109
 CHAPTER 4: Large-Scale Habitat Variables as Predictors of Benthic Fish Abundance in Riffles	 113
Introduction	113
Methods	116
Field data collections	116
Density estimation	116
Habitat measurements	118
Statistical analysis	119
Results	121
Riffle size and fish density	121
Adjacent unit habitat variables and fish density	123
Combined models	126
Discussion	130
Riffle size and fish density	130
Spatial proximity of patches, patch size, and fish density	132
Combined models	136
 SUMMARY AND MANAGEMENT IMPLICATIONS	 139

LITERATURE CITED	143
VITA	159

LIST OF FIGURES

Figure 1. Study reach in the mainstem Roanoke River in and around Salem and Roanoke, Virginia. Dark bars indicate the upstream and downstream extent of the area sampled.	9
Figure 2. Study reach in South Fork Roanoke River, Virginia. Dark bars indicate the upstream and downstream extent of the reach sampled.	10
Figure 1.1. Study sites sampled during 1991 on Roanoke River in Roanoke County, Virginia.	15
Figure 1.2. Study sites sampled during 1992 on South Fork Roanoke River in Montgomery County, Virginia.	17
Figure 1.3. Frequency distributions of perpendicular sighting distances for Roanoke darter (graphs 1A-1C), Roanoke logperch (graphs 2A-2C), and black jumprock (graphs 3A-3C) under low turbidity (graphs 1A-3A, NTU < 3.5), moderate turbidity (graphs 1B-3B, NTU ≥ 3.5 and < 5), and high turbidity (graphs 1C-3C, NTU ≥ 5) conditions. Note the break in the y-axis for graph 2C.	24
Figure 1.4. Box plots for Roanoke darter, Roanoke logperch, and black jumprock under low (NTU < 3.5), moderate (NTU ≥ 3.5 and < 5.0), and high (NTU > 5.0) turbidity conditions. The box encloses the middle 50% of the observations, the capped lines to the left and right of the box represent the 10% and 90% quantile, respectively, the squares to the left and right of the capped bars represent the 5% and 95% quantile, respectively, and the solid vertical bar in the box represents the median. Sample sizes are given in parentheses.	25
Figure 2.1. Study sites sampled during 1991 on Roanoke River in Roanoke County, Virginia.	44
Figure 2.2. Study sites sampled during 1992 and 1993 on South Fork Roanoke River in Montgomery County, Virginia.	46
Figure 2.3. Densities (number per 100 m ²) of Roanoke darter by class interval for depth, mean column velocity, substrate roughness, and	

level of siltation from the combined, Roanoke, and South Fork data sets. For depth and velocity, numbers on the ordinate represent interval mid-points. Abbreviations for substrate are F=fine, M=moderate, C=Coarse and for siltation are S=silted and U=unsilted. Significance levels of Kruskal-Wallis test for differences in median densities among intervals are given on each graph. 55

Figure 2.4. Densities (number per 100 m²) of Roanoke darter in each of the 21 multivariate habitat combinations from the combined, Roanoke, and South Fork data sets. Abbreviations on the ordinate for depth are S=shallow, M=moderate, and D=deep; for velocity S=slow, M=moderate, F=fast, A=all; for substrate F=fine, M=moderate, C=rough, A=all; for siltation S=silted, U=unsilted. Significance levels of Kruskal-Wallis test for differences in median densities among combinations are given on each graph. 56

Figure 2.5. Densities (number per 100 m²) of Roanoke logperch by class interval for depth, mean column velocity, substrate roughness, and level of siltation from the combined, Roanoke, and South Fork data sets. For depth and velocity, numbers on the ordinate represent interval mid-points. Abbreviations for substrate are F=fine, M=moderate, C=Coarse and for siltation are S=silted and U=unsilted. Significance levels of Kruskal-Wallis test for differences in median densities among intervals are given on each graph. 58

Figure 2.6. Densities (number per 100 m²) of Roanoke logperch in each of the 21 multivariate habitat combinations from the combined, Roanoke, and South Fork data sets. Abbreviations on the ordinate for depth are S=shallow, M=moderate, and D=deep; for velocity S=slow, M=moderate, F=fast, A=all; for substrate F=fine, M=moderate, C=rough, A=all; for siltation S=silted, U=unsilted. Significance levels of Kruskal-Wallis test for differences in median densities among combinations are given on each graph. 59

Figure 2.7. Densities (number per 100 m²) of black jumprock by class interval for depth, mean column velocity, substrate roughness, and level of siltation from the combined, Roanoke, and South Fork data sets. For depth and velocity, numbers on the ordinate represent interval mid-points. Abbreviations for substrate are F=fine, M=moderate, C=Coarse and for siltation are S=silted and U=unsilted. Significance levels of Kruskal-Wallis test for differences

in median densities among intervals are given on each graph. 60

Figure 2.8. Densities (number per 100 m²) of black jumprock in each of the 21 multivariate habitat combinations from the combined, Roanoke, and South Fork data sets. Abbreviations on the ordinate for depth are S=shallow, M=moderate, and D=deep; for velocity S=slow, M=moderate, F=fast, A=all; for substrate F=fine, M=moderate, C=rough, A=all; for siltation S=silted, U=unsilted. Significance levels of Kruskal-Wallis test for differences in median densities among combinations are given on each graph. 61

Figure 2.9. Habitat combination rankings of univariate (hatched bars) and multivariate (open bars) suitability indices for Roanoke darter from combined, Roanoke, and South Fork data sets. Abbreviations on the ordinate for depth are S=shallow, M=moderate, and D=deep; for velocity S=slow, M=moderate, F=fast, A=all; for substrate F=fine, M=moderate, C=rough, A=all; for siltation S=silted, U=unsilted. Significance levels are for test of correlation between suitability rankings (Spearman's correlation coefficient). 63

Figure 2.10. Habitat combination rankings of univariate (hatched bars) and multivariate (open bars) suitability indices for Roanoke logperch from combined, Roanoke, and South Fork data sets. Abbreviations on the ordinate for depth are S=shallow, M=moderate, and D=deep; for velocity S=slow, M=moderate, F=fast, A=all; for substrate F=fine, M=moderate, C=rough, A=all; for siltation S=silted, U=unsilted. Significance levels are for test of correlation between suitability rankings (Spearman's correlation coefficient). 64

Figure 2.11. Habitat combination rankings of univariate (hatched bars) and multivariate (open bars) suitability indices for black jumprock from combined, Roanoke, and South Fork data sets. Abbreviations on the ordinate for depth are S=shallow, M=moderate, and D=deep; for velocity S=slow, M=moderate, F=fast, A=all; for substrate F=fine, M=moderate, C=rough, A=all; for siltation S=silted, U=unsilted. Significance levels are for test of correlation between suitability rankings (Spearman's correlation coefficient). 65

Figure 2.12. Scatterplots of weighted usable area (WUA) calculated using both the univariate and multivariate suitability indices from the combined habitat use data set and abundance of Roanoke darter,

Roanoke logperch, and black jumprock at 28 sites sampled on the Roanoke and South Fork Roanoke Rivers in 1991, 1992, and 1993. Open circles represent the 12 South Fork samples, closed circles represent the 16 Roanoke River samples. P-values are given for significant correlations (Spearman's correlation coefficient, $P < 0.05$) between WUA and abundance from the 28 sites combined (C), the 16 Roanoke sites (R), and the 12 South Fork sites (S). 67

Figure 2.13. Roanoke darter, Roanoke logperch, and black jumprock scaled abundance and weighted usable area estimates from electrofishing sites sampled on the Roanoke River in 1991 and South Fork Roanoke River in 1992 and 1993. 78

Figure 3.1. Mean Roanoke darter densities (# of fish per cell) in target cells as a function of target cell suitability class and principal component score class. Scores from PCA are either high (H = greater than or equal to median score) or low (L = less than median score). The numbers in parentheses are the significance level of the Kruskal-Wallis test for overall differences in median densities among classes within a given suitability level. 93

Figure 3.2. Mean Roanoke logperch densities (# of fish per cell) in target cells as a function of target cell suitability class and principal component score class. Scores from PCA are either high (H = greater than or equal to median score) or low (L = less than median score). The numbers in parentheses are the significance level of the Kruskal-Wallis test for overall differences in median densities among classes within a given suitability level. 94

Figure 3.3. Mean black jumprock densities (# of fish per cell) in target cells as a function of target cell suitability class and principal component score class. Scores from PCA are either high (H = greater than or equal to median score) or low (L = less than median score). The numbers in parentheses are the significance level of the Kruskal-Wallis test for overall differences in median densities among classes within a given suitability level. 95

Figure 3.4. Scatterplots of Roanoke darter abundance (# of fish per site) versus area of suitable habitat (# of cells per site) and the join count ratio for the four levels of cell suitability defined in the text. Closed circles are from 16 Roanoke River sites sampled in 1991, open circles

are from the 12 South Fork Roanoke sites sampled in 1992 and 1993. P-values for significant univariate correlations (Pearson's correlation coefficient, $P < 0.05$) between abundance and both area and join count ratio are given on each graph for the combined data set (C), the Roanoke data set (R) and the South Fork data set (S). 96

Figure 3.5. Scatterplots of Roanoke logperch abundance (# of fish per site) versus area of suitable habitat (# of cells per site) and the join count ratio for the four levels of cell suitability defined in the text. Closed circles are from 16 Roanoke River sites sampled in 1991, open circles are from the 12 South Fork Roanoke sites sampled in 1992 and 1993. P-values for significant univariate correlations (Pearson's correlation coefficient, $P < 0.05$) between abundance and both area and join count ratio are given on each graph for the combined data set (C), the Roanoke data set (R) and the South Fork data set (S). 98

Figure 3.6. Scatterplots of black jumprock abundance (# of fish per site) versus area of suitable habitat (# of cells per site) and the join count ratio for the four levels of cell suitability defined in the text. Closed circles are from 16 Roanoke River sites sampled in 1991, open circles are from the 12 South Fork Roanoke sites sampled in 1992 and 1993. P-values for significant univariate correlations (Pearson's correlation coefficient, $P < 0.05$) between abundance and both area and join count ratio are given on each graph for the combined data set (C), the Roanoke data set (R) and the South Fork data set (S). 99

Figure 3.7. Scatterplot of Roanoke darter abundance (# of fish per site) versus both the join count ratio and area of suitable habitat for the combined data set at the 50% suitability level. The multiple regression equation quantifying the relationship among the variables is given in Table 3.4. 102

Figure 3.8. Scatterplot of Roanoke logperch abundance (# of fish per site) versus both the join count ratio and area of suitable habitat for the combined data set at the 5% suitability level and the Roanoke data set at the 5% suitability level. The multiple regression equations quantifying the relationship among the variables are given in Table 3.4. 103

Figure 3.9. Scatterplot of black jumprock abundance (# of fish per site) versus both the join count ratio and area of suitable habitat for the combined

data set at the 50% suitability level, the Roanoke data set at the 10% suitability level, and the South Fork data set at the 10% suitability level. The multiple regression equations quantifying the relationship among the variables are given in Table 3.4. 104

Figure 4.1. Areas sampled in South Fork Roanoke during 1992 and 1993. Hatched areas indicate reaches covered during the course of sampling. 117

Figure 4.2. Box plots of Roanoke darter, Roanoke logperch, and black jumprock densities in small, medium, and large riffles. The box encloses the middle 50% of observations, the capped vertical bars extend to the 10th and 95th percentiles, the open circles represent the 5% and 95% percentiles, and the horizontal bar in the box represents the median. 122

LIST OF TABLES

Table 1.1 Results of Theil-Sen regressions, correlations (Kendall's Tau), and paired t-tests for comparisons among Burnham, Emlen, quadrat, and strip transect density estimates for the Roanoke darter. For paired t-tests, value is estimated mean difference between the first and second member of each pair. Significance levels for Kendall's Tau and t-tests are given in parentheses. NS indicates $P > 0.05$	28
Table 1.2. Abundance estimates (#/ha) for Roanoke darter from Roanoke River sites sampled during 1991 (RR1 - RR5) and South Fork Roanoke sites sampled during 1992 (SF1 - SF9). For the Burnham estimates, confidence intervals are given in parentheses.	29
Table 1.3. Results of Theil-Sen regressions, correlations (Kendall's Tau), and paired t-tests for comparisons among Burnham, Emlen, quadrat, and strip transect density estimates for the Roanoke logperch. For paired t-tests, value is estimated mean difference between the first and second member of each pair. Significance levels for Kendall's Tau and t-tests are given in parentheses. NS indicates $P > 0.05$	30
Table 1.4. Abundance estimates (#/ha) for Roanoke logperch from Roanoke River sites sampled during 1991 (RR1 - RR5) and South Fork Roanoke sites sampled during 1992 (SF1 - SF9). For the Burnham estimates, confidence intervals are given in parentheses.	31
Table 1.5. Results of Theil-Sen regressions, correlations (Kendall's Tau), and paired t-tests for comparisons among Burnham, Emlen, quadrat, and strip transect density estimates for the black jumprock. For paired t-tests, value is estimated mean difference between the first and second member of each pair. Significance levels for Kendall's Tau and t-tests are given in parentheses. NS indicates $P > 0.05$	33
Table 1.6. Abundance estimates (#/ha) for black jumprock from Roanoke River sites sampled during 1991 (RR1 - RR3, RR5) and South Fork Roanoke sites sampled during 1992 (SF1 - SF9). For the Burnham estimates, confidence intervals are given in parentheses.	34
Table 2.1. Classification table used in developing the three-category substrate roughness variable.	49

- Table 2.2.** Habitat combinations and number of cells sampled in the development of the multivariate suitability indices. The first number given is the total number of cells sampled, the second is the number of cells sampled in Roanoke River and the third is the number sampled in South Fork Roanoke. Depth classes are shallow (<20 cm), moderate (≥ 20 cm and <40 cm), and deep (≥ 40 cm). Velocity classes are slow (<20 cm/s), moderate (≥ 20 cm/s and < 50 cm/s), and fast (≥ 50 cm/s). Fine, moderate, and coarse substrate classes and silted versus unsilted conditions are as defined in the text. . . . 51
- Table 3.1.** Variable loadings, eigenvalues, and proportion of variance explained for the three components retained by the principal components analysis of adjacent cell habitat characteristics for Roanoke darter. Separate analyses were conducted for target cells classified as poor, fair, good or excellent habitat based on multivariate suitability values developed in Chapter 2. Table entries are variable loadings and dashes indicate loadings between 0.399 and -0.399. The number of target cells used in each analysis are given in parentheses. 89
- Table 3.2.** Variable loadings, eigenvalues, and proportion of variance explained for the three components retained by the principal components analysis of adjacent cell habitat characteristics for Roanoke logperch. Separate analyses were conducted for target cells classified as poor, fair, good or excellent habitat based on multivariate suitability values developed in Chapter 2. Table entries are variable loadings and dashes indicate loadings between 0.399 and -0.399. The number of target cells used in each analysis are given in parentheses. 90
- Table 3.3.** Variable loadings, eigenvalues, and proportion of variance explained for the three components retained by the principal components analysis of adjacent cell habitat characteristics for black jumprock. Separate analyses were conducted for target cells classified as poor, fair, good or excellent habitat based on multivariate suitability values developed in Chapter 2. Table entries are variable loadings and dashes indicate loadings between 0.399 and -0.399. The number of target cells used in each analysis are given in parentheses. 91
- Table 3.4.** Significant multiple regression models relating area of suitable habitat (ARE) and the join count ratio (JNCT) to Roanoke darter, Roanoke logperch, and black jumprock abundance from all 28 sites

sampled in 1991, 1992, and 1993 (Combined data set), the 16 Roanoke River sites sampled in 1991 (Roanoke data set), or the 12 South Fork Roanoke sites sampled in 1992 and 1993 (South Fork data set). Suitability level indicates the proportion of cells designated as suitable habitat. Coefficient P-values are based on partial t-tests and the model P-values are based on the overall F-test. R^2 is the coefficient of multiple determination. Scatterplots displaying the raw data are presented in Figures 3.7 (Roanoke darter), 3.8 (Roanoke logperch) and 3.9 (black jumprock). 100

Table 4.1. Correlation coefficients (Spearman's ρ) between fish densities in individual riffles and macrohabitat variables for the entire data set, and for 3 subsets based on riffle size. P-values are given in parentheses for significant correlations ($P < 0.05$.) 124

Table 4.2. Significant regression models accounting for the greatest variance in Roanoke darter densities for the full data set and for reduced data sets based on the size of the target riffle. Abbreviations are PDEP = Pool depth, PVEL = Pool velocity, PSUB = Pool substrate, RSUB = Riffle substrate, TRARE = Total riffle area. 125

Table 4.3. Significant regression models accounting for the greatest variance in Roanoke logperch densities for the full data set and for reduced data sets based on the size of the target riffle. Abbreviations are TPARE = total pool area, PSUB = pool substrate, PDEP = pool depth, PVEL = pool velocity, RDEP = riffle depth, RVEL = riffle velocity. 127

Table 4.4. Significant regression models accounting for the greatest variance in black jumprock densities for the full data set and for reduced data sets based on the size of the target riffle. Abbreviations are TRARE = total riffle area, PDEP = pool depth, PSUB = pool substrate, RDEP = riffle depth, RVEL = riffle velocity. 128

Table 4.5. Significant multi-scale multiple regression models accounting for the greatest variance in Roanoke darter, Roanoke logperch, and black jumprock abundance (number of fish per site) for the for 15 electroshocking sites sampled in the Roanoke River in 1991 and the South Fork Roanoke in 1992 and 1993. Abbreviations are TRARE = total riffle area, PDEP = pool depth, RSUB = riffle substrate,

RVEL = riffle velocity, MVWUA = weighted usable area using the multivariate suitability index, and AREA50 = area of suitable habitat using the 50% suitability criteria. 129

Introduction to the Dissertation

A basic objective of disciplines in applied ecology (i.e. conservation biology, forestry, fisheries and wildlife management) is to determine the effect of human activity on the distribution and abundance of natural resources. Given the range of potential impacts and the diversity of organisms, communities, and ecosystems subject to alteration, case by case assessment of impacts is an unreasonable undertaking. Resource management scientists therefore attempt to develop general models of impacts on target organisms, communities, or ecosystems in order to predict, and perhaps ameliorate, the effects of anthropogenic activities on natural systems.

Historically, resource management models focused on harvest level manipulation and alteration or enhancement of the physical environment to manage resource levels (Nielsen 1993). As the focus of resource management expanded to include non-consumptive uses, traditional population-yield models (i.e. Beverton and Holt 1957, Ricker 1975) became less germane, while habitat manipulation (both intentional and unintentional) came to the forefront. The focus on habitat by managers was complemented by the breadth of basic ecological research relating the distribution and abundance of a variety of organisms to aspects of their physical environment. As a result many of the more common management models employed today relate some measure(s) of the physical environment to a measurable response in an identified state variable. These models (generally referred to as habitat models) assume that quantified physical variable(s) either control a state variable directly (i.e., limitation of a critical resource) or act as a surrogate for a factor performing a similar function.

Stream fish biologists have demonstrated that the distribution and abundance of fish can be related to the types of habitat available in a given body of water

(Gorman and Karr 1978, Orth and Maughan 1982, Moyle and Baltz 1985, McClendon and Rabeni 1987). Fish species use similar habitat resources in differing ways (Grossman et al. 1987, Dolloff and Reeves 1990, Kessler and Thorp 1993) and in some instances, single habitat variables may limit a specific life stage and thereby determine density and abundance (Power 1984, Newman and Waters 1989, Greenberg and Stiles 1993, Sabo 1993). In other cases, multiple habitat variables may interact to determine suitable and unsuitable areas for a given species (Warren et al. 1991, Taylor et al. 1993). Although many studies have focused on habitat variables measured at, or in close proximity to, the point where a fish is observed or captured (Moyle and Baltz 1985, Bain and Finn 1991, Freeman and Freeman 1994), habitat characteristics at larger spatial and temporal scales may also be important (Sheldon 1968, Horwitz 1978, Evans and Noble 1979, Capone and Kushlan 1991, Freeman and Grossman 1993, Leftwich 1994).

Large-scale models usually concentrate on species richness (Sheldon 1968, Whiteside and McNatt 1972, Horwitz 1978, Evans and Noble 1979), community composition (Whittier et al. 1988, Lyons 1989, Warren et al. 1991, Taylor et al. 1993), or total fish biomass (Binns and Eisermann 1979, Layher 1983, Bowlby and Roff 1986, Layher and Brunson 1992). The predictions generated by these models are general and reasonably precise although the causal factors are subject to much speculation and debate (Grossman et al. 1982, Mahon 1984, Ross 1986, Matthews 1986, Matthews and Heins 1987, Schlosser 1990, Schlosser 1991). In contrast, fine-scale models usually focus on the distribution and/or abundance of populations, stocks, or single species (Orth and Maughan 1982, Shirvell and Dungey 1983, Moyle and Baltz 1985, Heggenes 1988, Barrett and Maughan 1994) or resource-use guilds (Leonard and Orth 1988, Kinsolving and Bain 1993, Austen et al. 1994, Travnichek and Maceina 1994, Vadas 1994). These models often have good predictive capability for the species in the system that provided the calibration data

set but perform poorly when applied to other systems (Fausch et al. 1988, Shirvell 1989).

The utility of habitat models for resource managers comes from a number of factors, but at a minimum, a useful habitat model; 1) should be based on logically sound, biologically reasonable functions, 2) contain variables that can be influenced by resource managers, 3) should be relatively simple, 4) have reasonable data acquisition costs, and 5) have general applicability but provide specific predictions (Salwasser 1986, Fausch et al. 1988, Bain and Boltz 1989, Van Horne and Wiens 1991). Given these criteria, available models have obvious shortcomings. Large-scale models of community composition and fish distribution are the most general models available and have relatively high predictive capability, but managers can do little to influence the variables commonly included (for example, elevation, stream order, temperature regime, ecoregion). In contrast, the most successful and widely used fine-scale model (the Instream Flow Incremental Methodology [IFIM]) directly addresses changes in fish populations associated with flow alteration, a variable that is commonly manipulated by resource managers, water supply managers, and power companies (Stalnaker et al. 1995). IFIM has been successful only in instances where extensive knowledge of the life history and potential limiting life stages or resources is available for the target species.

The ideal habitat model would combine the general predictive capability of large-scale models with the ability of the IFIM model to predict changes in abundance with changes in flow. The assumption of IFIM (and many similar fine-scale models) that a single resource or life-stage always limits a given population is unreasonable. The overall fitness of an organism is a function of a number of interacting factors, operating at a variety of spatial and temporal scales. For example, the immediate foraging success of an individual often is a function of the availability of food resources and the presence of refuge from potential predators.

Traditional fine-scale measures of suitability may reflect this immediate need well. Alternatively, the foraging success of an individual over longer time periods may be a function of processes at larger spatial and extended temporal scales. Questions of prey depletion, interaction with potential inter- and intra-specific competitors, and the temporal and spatial variability in system productivity become important. At longer temporal scales, larger spatial scales may become important as the availability of winter refuge habitat and the distribution of suitable spawning and nursery habitat come into play. This is a reflection of the complex life histories of many stream fish and their need for differing types of resources at different points in their development (Schlosser 1991).

Connell and Sousa (1983) suggested that assessments of community stability and persistence be based on data collected over a period of time at least as long as the twice the generation time of the longest-lived member species. A similar argument can be made for habitat studies that attempt to assess the factors that determine the distribution and abundance of a single species. This is essentially what has occurred in the instances where microhabitat models have been successfully implemented, as the sum total of basic research on highly valued game species has created data sets extending across multiple generations. Unfortunately, management agencies (or graduate students for that matter) rarely have the luxury of carrying studies over such extensive time periods.

A reasonable alternative to the temporally extensive studies needed to develop adequate microhabitat models is to establish the temporal stability of physical habitat characteristics that could play a role in population regulation and assess the relationship between species abundance and those habitat features that persist up to a temporal scale longer than twice the generation time of the target species. Although changes in physical habitat at temporal scales longer than that experienced by two generations occur (i.e. global warming, forest regrowth), those changes fall into the

realm of long-term adaptation, not short-term population regulation and are therefore beyond the scope of this study. Southwood (1977) suggested a view of habitat as a templet for ecological strategies very similar to this, suggesting that it might be possible to develop a "periodic table" of species types based jointly on the spatial grain of species habitat response and the temporal persistence of those habitats. Along the same lines, Winemiller and Rose (1992) have proposed a classification of fish life history strategies that arrays species on a three-dimensional response surface based on the stability, persistence, and predictability of environmental variation of the species' environment.

The temporal persistence and stability of physical habitat features in lotic waters are a function of the interactions between climate, geology, and geomorphology (Brussock et al. 1985, Poff and Ward 1989, Poff and Ward 1991). Frissell et al. (1986) proposed a hierarchical framework of stream habitat features based on these factors and although the classification was originally developed for second and third order montane streams in the Pacific Northwest, it has proven to be broadly applicable to temporally persistent flowing waters in many regions of the United States. Their classification is particularly useful in the current context, because it integrates both temporal persistence and spatial extent of habitat features which are potentially important to stream organisms. Since the vast majority of stream fish have lifespans shorter than a decade, habitat characteristics that have persistence times of up to 20 years should be useful in developing habitat models designed to take into account the importance of multiple spatial scales in predicting population abundance.

Not surprisingly, the most ephemeral scale of physical habitat identified by Frissell et al. (1986) is the combination of depth, velocity, substrate, and cover typically measured in most fish habitat studies and commonly termed microhabitat. Depending on the system, rough bounds on the spatial extent of microhabitat range

from 10^{-1} to 10^1 m², while the temporal persistence ranges from minutes during the rising limb of a flood in a flashy stream to months in a groundwater-fed spring creek. The next level in the hierarchical classification is erosional/depositional units, extending spatially from 10^1 to 10^4 m², persisting temporally from years to decades, and commonly referred to as mesohabitat or pool/riffle sequences. Given the short lifespans of stream fish, these are the two levels in the hierarchy that are potentially important within the framework I have developed thus far, since the persistence times of spatial units at higher levels in the hierarchy is well beyond two decades.

Given this background, my goal in this study was to assess the utility of multiple habitat scales for predicting abundance of stream fishes. To do this, I developed models relating fish abundance to habitat availability at three separate spatial scales, including 1) the commonly accepted microhabitat scale, 2) an intermediate scale that encompassed the distribution of microhabitat within individual mesohabitat units, and 3) a large scale that addressed the spatial distribution and abundance of mesohabitat units. Once the best model at each spatial scale was defined, the models were combined to determine the additional explanatory power gained by combining habitat measures across measurement scales. Models at all three scales were developed for three species with differing life history strategies (*sensu* Winemiller and Rose 1992) in order to assess potential interactions among life history, abundance, and habitat utilization.

This dissertation is divided into four studies. The first study (Chapter 1) was methodological and motivated by the need for a rapid, efficient method of assessing riffle fish abundance over large spatial scales (numerous riffles). In this study, I determined the adequacy of underwater observation as a density estimation technique for benthic riffle fish. In the second study (Chapter 2), in addition to developing microhabitat models, I also explored the question of whether fish respond independently to depth, water velocity, and substrate composition, or whether

interactions among these variables was important in the types of habitat fish select. In the third study (Chapter 3), I attempted to step up one level from traditional microhabitat models by using types of habitat surrounding the point where a fish occurred as a measure of habitat suitability instead of the habitat at the point where the fish was actually found. A second objective in this study was to explore the value of using the spatial distribution of patches of suitable and unsuitable habitat within a riffle as an indicator of the riffle's potential to support high densities of the target species. The fourth study (Chapter 4) developed a mesohabitat-based model of fish abundance based largely on concepts drawn from landscape ecology. In each of the final two chapters, I took the best models from each of the preceding chapters and combined them into a single model of riffle suitability in order to determine if any additional explanatory power was gained by investigating habitat relationships across multiple scales.

Study Area

All portions of all studies were carried out in upper Roanoke River in Roanoke and Montgomery Counties, Virginia, in the Valley and Ridge physiographic province (Jenkins and Burkhead 1994). The geomorphologic channel form is primarily gravel-bed (Brussock et al. 1985) with well-developed pool-riffle sequences. Inspection of 90 years of flow records from a gaging station located just below the lower boundary of the study area showed flow had been continuous during the period of record (Prugh et al. 1990), annual flow was relatively predictable, and floods were relatively infrequent and unpredictable. These characteristics correspond to the mesic groundwater streamflow class of Poff and Ward (1989). Although there are no major dams in the study area, there are numerous small low-head dams and low-water bridges throughout the watershed which might limit fish movement during low flow periods. The upper Roanoke is the farthest downstream, moderate-size, free flowing section of the river, but the impoundment associated with Niagara

Dam, the first major obstruction to flow on the Roanoke, begins at the mouth of Tinker Creek, approximately 4 km below the downstream end of the study area (Figure 1). A number of municipalities in Roanoke County recently completed construction of a water supply project (Spring Hollow Reservoir) which could alter flow regimes in the future.

Sampling was carried out in two separate reaches. The first reach was located on mainstream Roanoke River in Roanoke and Salem, Virginia (Figure 1). The area bordering the reach is primarily urban, with commercial, manufacturing, and high density residential housing being the dominant land uses. Despite the high level of anthropogenic development, much of the riparian zone is vegetated, with willows (*Salix* spp.), hackberry (*Celtis occidentalis*), and sycamore (*Plantanus occidentalis*) being the dominant woody species. Data from a gaging station just below the downstream end of the study reach show a watershed area of 1023 km² and a mean daily flow of 10.54 m³·s⁻¹ (Prugh et al. 1990). Based on measurements taken during late summer base flow conditions, average stream width is 24.9 m, average pool depth is 75 cm and maximum depth in most pools is less than 2 m, although there are some pools with maximum depths exceeding 4 m. Stream gradient in the reach is 1.8 m·km⁻¹.

The second study reach was located on South Fork Roanoke River in Montgomery County, Virginia (Figure 2). Land use in this portion of the watershed is primarily agricultural, with much of the land in pasture or woodland. The riparian zone is largely vegetated, with dominant woody species similar to those found along the mainstem section. Data from a gaging station in the upper portion of the study reach indicate a watershed area of 285 km² and a mean daily flow of 3.14 m³·s⁻¹ (Prugh et al. 1990). Average stream width in the reach is 16.7 m, average pool depth is 53 cm, and maximum pool depth is usually less than 1.5 m although some pools have maximum depths exceeding 3 m. Stream gradient in the reach is 2.7

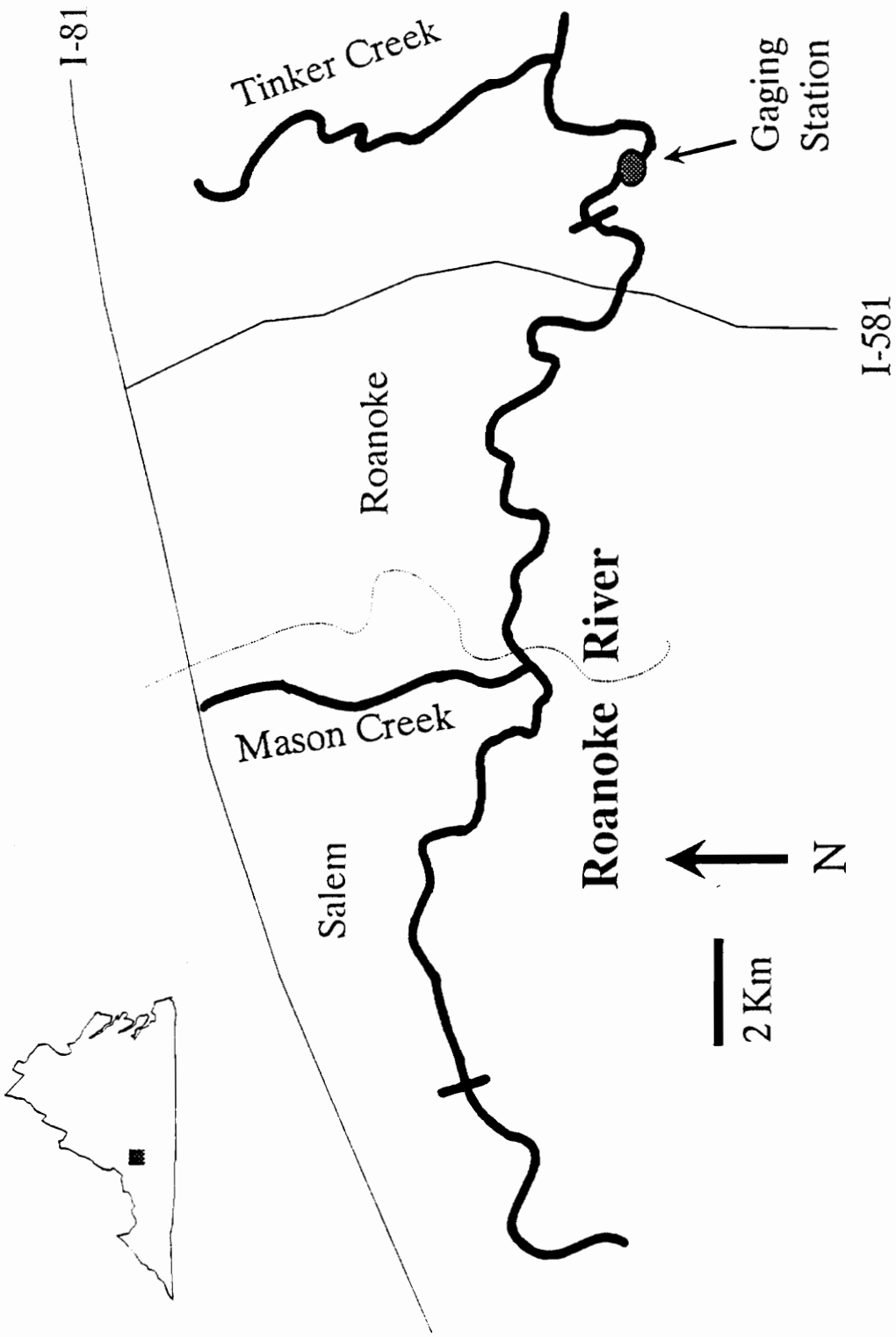


Figure 1. Study reach in the mainstem Roanoke River in and around Salem and Roanoke, Virginia. Dark bars indicate the upstream and downstream extent of the area sampled.

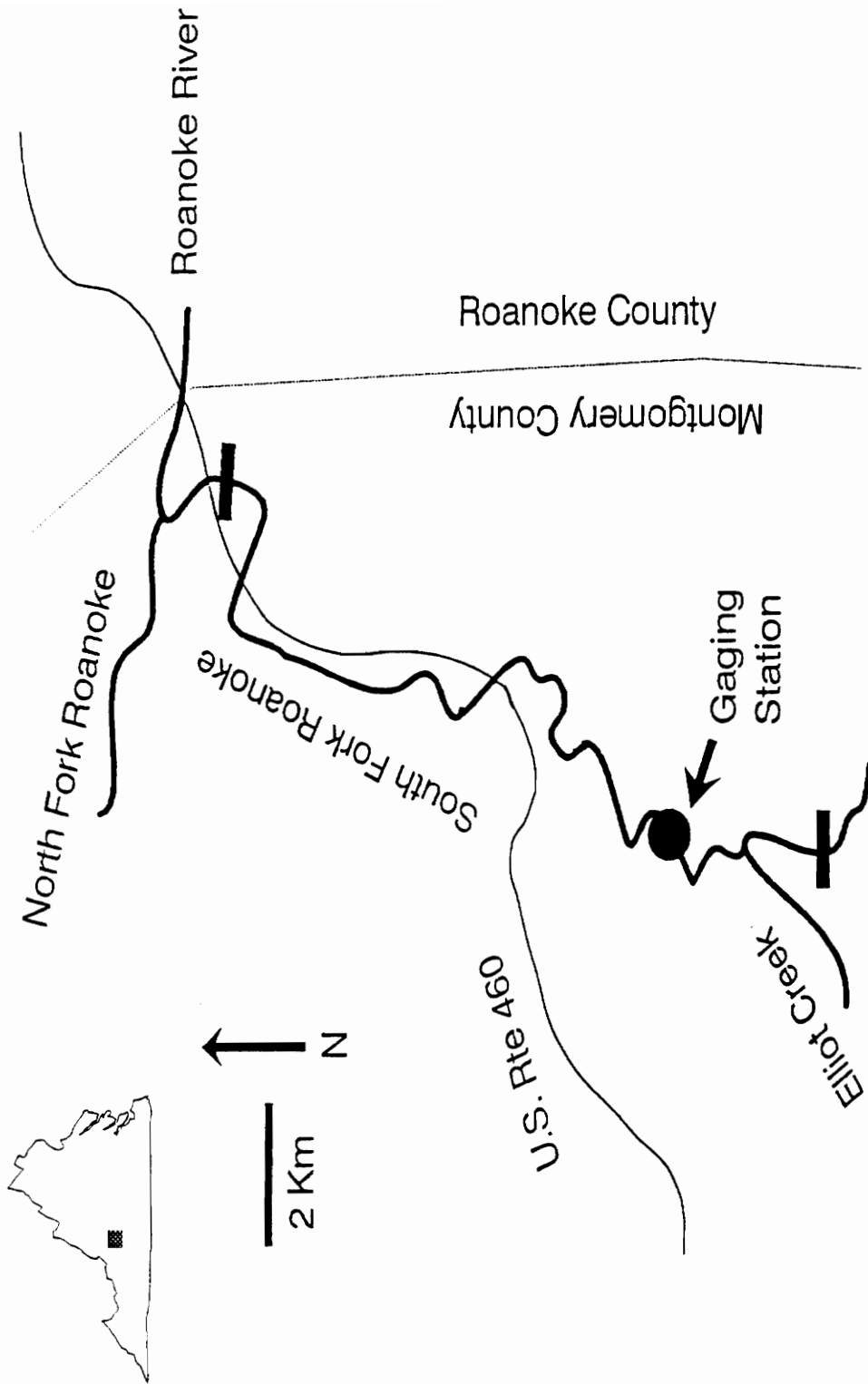


Figure 2. Study reach in South Fork Roanoke River, Virginia. Dark bars indicate the upstream and downstream extent of the reach sampled.

m·km⁻¹.

All sampling was carried out during summer and early fall months. Furthermore, only adults of the three study species I will describe in the next section were sampled. This represented a compromise between ecological and logistic considerations. Although there is abundant evidence that young-of-year and juvenile stream fish may have habitat requirements that differ from their adult counterparts and that there may be seasonal differences in habitat use by stream fish, management agencies rarely have the luxury of undertaking the extensive sampling necessary to establish these relationships. In contrast, adult fish are easier to sample, and the resulting abundance estimates are usually more precise. The choice to sample only during summer stemmed from similar concerns. Since the overall goal of this dissertation was not just to examine the potential advantages of sampling across multiple scales, but also to develop methods that could be applied to other species and systems, I chose a sampling scheme that would be relatively easy to apply.

Study Species

The three species in these studies, Roanoke darter (*Percina roanoka*), Roanoke logperch (*P. rex*), and black jumprock (*Scartomyzon cervinus*) were selected to minimize differences in general habitat, reproductive (sensu Balon 1975), and trophic guild status while maximizing differences in life history characteristics used by Winemiller and Rose (1992). All three species are benthic insectivores found primarily in erosional habitats during summer low flow and can be characterized as simple lithophilic spawners (Balon 1975, Matthews 1990, Jenkins and Burkhead 1994).

In contrast to similarities in resource use characteristics commonly used to define guild status, the three species exhibit differences in life history characteristics that place them at different points on the adaptive surface proposed by Winemiller

and Rose (1992). Roanoke darter is a small (maximum total length [TL] = 70 mm), short-lived (maximum age = 3 years) species that becomes reproductively mature in the spring of the first year following hatching (Jenkins and Burkhead 1994).

Although there is little information on fecundity for P. roanoka, other members of the subgenus Alvordius produce from 600-1700 ova, with counts of mature ova ranging from 260-400 per female (Page 1983). The combination of small adult body size, rapid maturation, early reproduction, and relatively high size-specific fecundity place Roanoke darter at the opportunistic end of the life-history surface.

Roanoke logperch is one of the largest (maximum TL = 160 mm) and longest-lived (maximum age = 6 years) members of the tribe Etheostomatini (Page 1983, Burkhead and Jenkins 1994). Although males become reproductively mature in their second year, the majority of females do not mature until their third year and produce from 180-600 mature ova (Burkhead and Jenkins 1994). In comparison to Roanoke darter, the larger adult size, longer life span and delayed maturity of the logperch push it towards the periodic life-history strategy.

Black jumprock is one of the smaller members (maximum TL = 220 mm) of the family Catostomidae and has a relatively short life-span (maximum age = 5 years). Both males and females mature at age 2 and although fecundity data is lacking for this species, females of similar-sized species in the closely-related genus Thorburnia produce 700-2000 mature ova per year (Etnier and Starnes 1993, Jenkins and Burkhead 1994). In comparison to the other two species, black jumprock is considered intermediate between the opportunistic and periodic strategies.

CHAPTER 1

Use of line transect methods to estimate abundance of benthic stream fishes.

Introduction

Underwater observation is well-established in the Pacific Northwest as a method of estimating distribution and abundance of salmonids (Northcote and Wilkie 1963, Schill and Griffith 1984, Slaney and Martin 1987). It has also been used successfully in surveys of abundance of lacustrine (Keast and Harker 1977, Turner and Mackay 1985) and marine reef species (Sale and Douglas 1981, Thresher and Gunn 1986) and has proven to be efficient, reliable, precise, and accurate. Where comparisons with traditional methods (e.g. depletion estimation, mark-recapture, use of toxicants) have been carried out, underwater observation often performs as well or better than the traditional techniques, with a significant reduction in effort.

Use of underwater observation for surveys of benthic species has been limited and information on the precision and reliability of estimates is lacking. The fact that underwater observation is not a common technique for assessing benthic species abundance may be due to assumptions associated with its more usual application to large, highly visible species in waters of good clarity. Most of these studies assume that all fish in a strip of set width are visible and therefore a total count is possible for that strip. Density is estimated by dividing the number of fish counted by the area sampled (Keast and Harker 1977, Schill and Griffith 1984, Turner and MacKay 1985), analogous to the strip transects used in wildlife studies (Seber 1982). In some instances, visual counts have been adjusted using correction factors based on estimates obtained with alternative estimation techniques (i.e. three-pass depletion estimates) under similar conditions. In contrast to many of the highly

visible water column species typically assessed with direct observation, benthic species are often small, cryptically-colored forms living in complex habitats where it may not be possible to designate a strip where all targets are seen with certainty.

An alternative to strip transect estimation is to use a group of models based on distance sampling (Eberhardt 1968, Eberhardt 1978, Burnham et al. 1980, Buckland et al. 1993), specifically those based on line transects. Although used in wildlife studies for over 40 years and more recently in the study of marine mammals, these models have only sporadically been applied to studies of fish populations (Thresher and Gunn 1986, Bergstedt and Anderson 1990). Rather than assuming that the probability of seeing a target is 1.0 out to the limits of observer visibility, line transect models assume that only those targets near the observer are seen with certainty. Then, as the distance between the target and the observer increases, the probability of seeing the target decreases. The central problem with these models is estimation of a function that adequately characterizes sighting probability as distance from the observer increases.

My objectives in this study were to 1) determine whether line transect or strip transect models provide an appropriate conceptual approach for the estimation of abundance of benthic stream fishes, 2) compare estimates of abundance calculated from two different line transect sampling models, and 3) compare the estimates obtained from the line transect models with those obtained using two traditional methods, electrofishing and the strip transects.

Methods

Study area and study species

The study was conducted on the Roanoke River in Roanoke County and the South Fork Roanoke River in Montgomery County, VA. Five sites were sampled on the Roanoke river during August, September, and October 1991 (Figure 1.1), and nine sites were sampled on the South Fork Roanoke during August and September

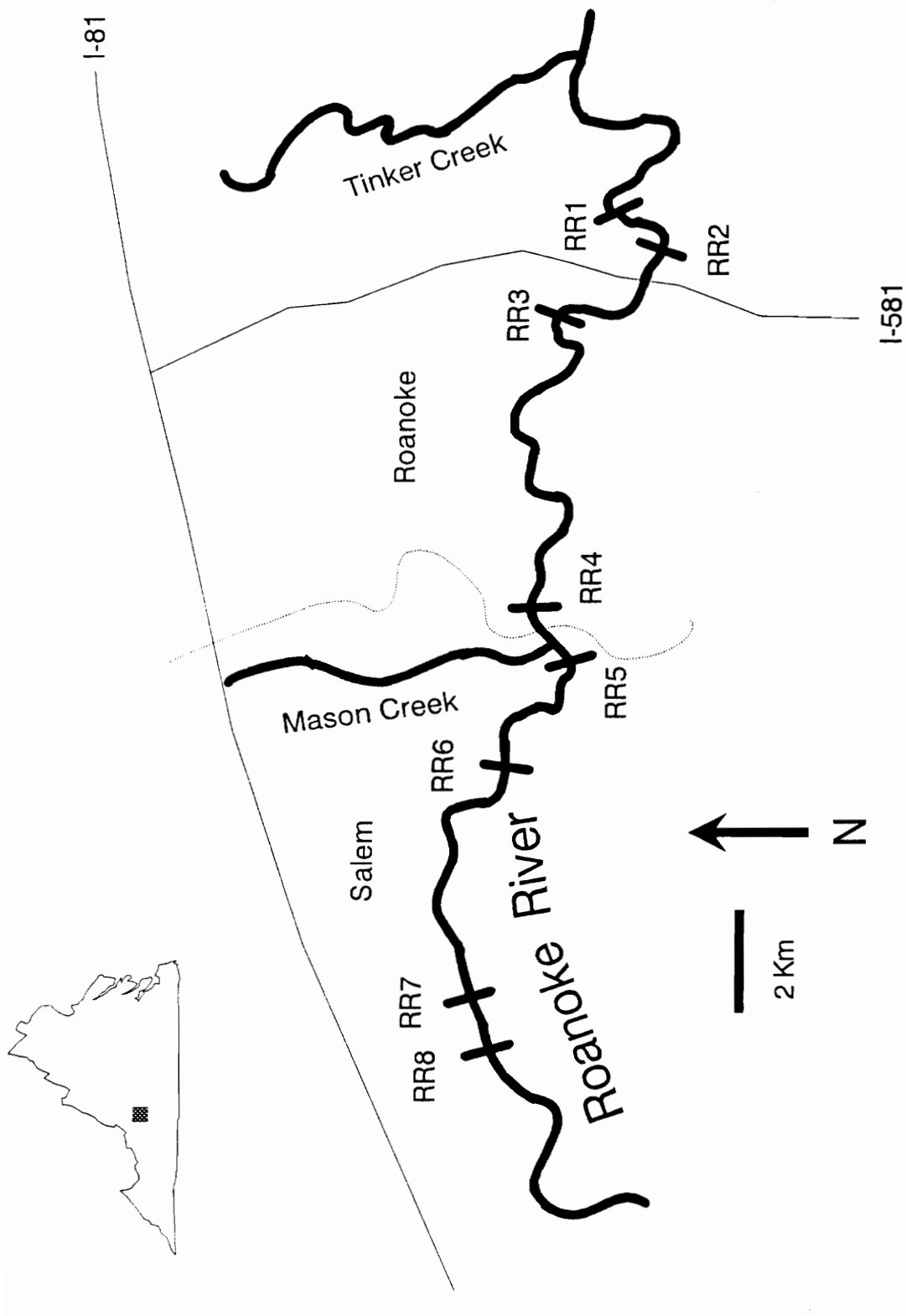


Figure 1.1. Study sites sampled during 1991 on Roanoke River in Roanoke County, Virginia.

1992 (Figure 1.2). As the three target species for this study were benthic riffle fishes, each of the sites included at least one full riffle-run sequence. Most of the sites also included the tail and head of the adjoining upstream and downstream pools. Study sites ranged in length from 130 m to 168 m and in average width from 13.5 m to 24.7 m.

The three species exhibit behavioral and morphological differences. The Roanoke darter (*Percina roanoka*) is small (40-70 mm TL), cryptically colored, relatively solitary, and tends to remain stationary when approached by a snorkeler. Movements are usually in short, rapid bursts. The Roanoke logperch (*P. rex*) is similar to the Roanoke darter, but is larger (60-140 mm TL) and less tolerant of snorkelers. The black jumprock (*Scartomyzon cervinus*) is larger still (70-220 mm TL), uniformly colored, tends to move continuously, and occurs either singly or in groups of up to 40 individuals. Of the three study species, the jumprock is the most difficult to approach without disturbance.

Underwater observation

Ensuring that observers' passage through the study area is along a well-defined line of travel and that measurements of distance from that line to the location of observed targets are both precise and accurate are key concerns in line transect studies. To meet these criteria, parallel lines oriented along the flow of the river were marked by yellow nylon twine on the day of sampling. Between two and five lines were located at each site depending on the width of the area to be sampled. Spacing between lines was based on water clarity and was a minimum of 1.5 times maximum visibility on the day of sampling. Maximum visibility was determined in one of two ways. During 1991, a Secchi disk was suspended vertically in the water column in front of a snorkeler. The snorkeler moved away from the disk until it was no longer visible. The distance between the snorkeler and the disk was measured and served as the maximum visibility for that day. There was a strong

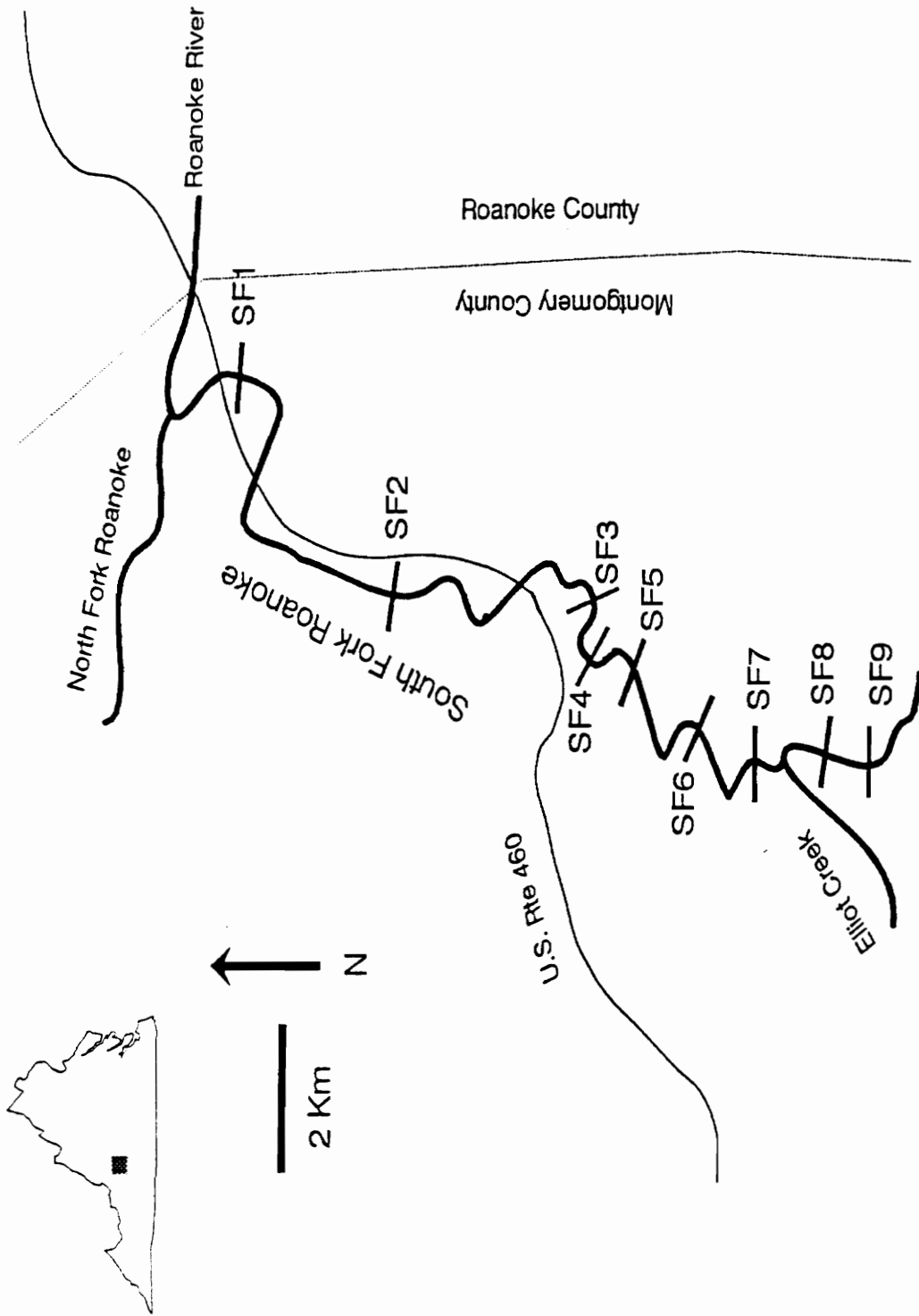


Figure 1.2. Study sites sampled during 1992 on South Fork Roanoke River in Montgomery County, Virginia.

correlation ($r^2 = 0.99$, $P < .001$) between maximum visibility and turbidity, measured in nephelometric turbidity units (NTU) by a Hach Model 940 turbidimeter. During 1992, turbidity measurements served as a surrogate for maximum visibility.

Following placement of the transect lines, snorkelers entered the water downstream of the area to be sampled and one snorkeler moved slowly upstream along each of the lines, keeping the centerline of the body over the nylon twine. Each observer scanned the stream bottom directly in front and to both sides of the line of travel. When one of the three target species was sighted, a weighted marker was placed on the stream bottom at the location where the fish was first spotted. Markers were color-coded by species and numbered to allow identification of markers from different passes on the same day. Given that the spacing between lines resulted in some overlap between transects, double counting of fish was avoided by having adjacent observers remain abreast of each other. When a fish was observed in an area of potential overlap, communication between observers ensured that only one marker was placed for that fish. Depending on time, weather, and availability of personnel, 1 to 8 complete passes (a single pass encompassing snorkeling each of the individual lines one time) were made through each site. On days when more than one pass was made through a site, a minimum of one hour separated the completion of one pass and the initiation of the next. This "rest period" allowed fish to recover from disturbance caused by the preceding snorkeling pass. Upon completion of all snorkeling passes on a given day, the perpendicular distance of each marker from the transect line, species, transect number, and pass number were recorded.

Electrofishing

I also used a quadrat-based electrofishing technique with a Coffelt BP-6 AC backpack electrofishing unit and a seine 4.5 m long, 1.5 m deep, with mesh size of 0.6 cm, and a 1.5 by 1.5 by 1.5 m bag attached. The location of quadrats at each site was determined systematically. Quadrats were approximately rectangular with

width of 4 m and length of 10 m, giving a total area sampled in each quadrat of 40 m². Starting at the downstream end of each site, sampling proceeded upstream along a series of transects placed perpendicular to the streamflow at 15-m intervals. The first quadrat on each transect was placed at least 2 m from the adjacent bank. The adjoining edges of quadrats along the same transect were at least 2 m apart. The number of quadrats along a given transect was a function of stream width at that transect and the criteria previously mentioned. Upstream and downstream limits for quadrats on a given transect were marked by placing fluorescent tape on the stream bank at the appropriate point, while the center of a quadrat was identified by placing a weighted fluorescent marker on the stream bottom.

Following location of the quadrat, the seine was held downstream of the area to be sampled. Once the net was in place, the area immediately upstream of the net was thoroughly shocked. Following completion of the electrofishing pass, the net was lifted and all target species retained in the net were identified and counted. The area shocked was visually inspected to ensure that all stunned fish had been carried into the net. Fish remaining on the stream bottom within the quadrat were retrieved and included in the sample. In all cases personnel avoided wading through quadrats prior to sampling. Spacing and location of quadrats and techniques used during setting and lifting of the bag seine were designed to minimize disturbance of areas to be shocked.

Density Estimation

As stated earlier, the central problem in distance sampling is the specification of the form of the sighting function. Numerous models, varying in their underlying assumptions, have been developed to address this issue (reviewed in Buckland et al. 1993). At one extreme are models that make few assumptions about the shape of the sighting function. The distribution of sighting distances is used to fit the best function for the data. These models are statistically robust but reliable estimates of

the sighting function can only be obtained with fairly large sample sizes.

At the other extreme are conceptually simple models that depend on restrictive assumptions about the shape of the sighting function. Although such models require fewer observations, minor violation of the underlying assumptions may result in markedly biased estimates. Furthermore, these simpler models lack the strong statistical foundation of the data-intensive models and estimation of their precision (i.e. variance) is problematic. The models used in this study represent the two extremes of the potential models.

The first model I used was a line transect approach developed by Burnham et al. (1980) that uses the Fourier series (Crain et al. 1979) to estimate density. It makes few assumptions about the shape of the sighting function. The formula for density estimation is:

$$D = n * (f(0)/2L); \quad (1)$$

where L = length of line sampled (m); n = the number of each target species detected; $f(0)$ = the function $f(x)$ evaluated at 0 distance from the transect line. The function $f(x)$ is the estimated probability density function for the target species evaluated at distance = x .

Robust estimation of $f(0)$ requires a minimum of 40 observations, and sample sizes greater than 80 are preferable. Few of the site/species combinations in this study yielded observation numbers of that magnitude, so it was necessary to pool observations across sites to obtain valid estimates of $f(0)$. Pooling of observations across sites is acceptable if it can be assumed that conditions influencing the shape of the sighting function are consistent across the pooled sites (Buckland et al. 1993). Experience during sampling indicated that both fish behavior and observer efficiency varied as a function of turbidity levels, so sites were divided into three groups based on turbidity levels on the day of sampling and an estimate of $f(0)$ developed for each species/turbidity level combination. Low turbidity sites were those with NTU

readings less than 3.5, moderate turbidity sites were those with NTU readings from 3.5 - 5.0, and high turbidity sites were those with NTU readings greater than 5.0. Pooling of sites in this manner yielded sample sizes for each of the turbidity level/species combinations greater than 40, with the exception of Roanoke logperch at high turbidity sites where the sample size was only 29. The data sets were further modified prior to modelling of $f(0)$ by excluding the upper 5% of observations from each of the species/turbidity classes. These upper outliers have little if any effect on the final density estimate and their exclusion leads to lower variance and better model fit for the function $f(0)$ (Burnham et al. 1980, Buckland et al. 1993). Estimates of the sampling variance of each of the site/species combinations were obtained using the equation:

$$\text{var}(D) = D^2 [\text{CV}(n)^2 + \text{CV}(f(0))^2]; \quad (2)$$

where CV = coefficient of variation ($100 \cdot \text{SE}/\text{mean}$).

For all sites, the number of replicate lines was less than or equal to five, yielding poor estimates of $\text{var}(n)$, so it was assumed that $\text{var}(n)=2n$ (Burnham et al. 1980). Log-based 95% confidence intervals were calculated for each of the site/species density estimates. All calculations were carried out using the program DISTANCE (Laake et al. 1993).

The second density estimation model is based on an approach popularized by Emlen (1971) for surveys of songbirds. The Emlen model assumes that the probability of seeing a target is equal to 1.0 out to some minimum distance from the observer. Beyond this minimum distance, sighting probability declines out to some boundary width beyond which no targets are observed. Given this assumption, a smoothed frequency distribution of sighting distances should exhibit a flat shoulder proximal to the y-axis. The point at which the frequency distribution begins to dip defines the distance at which sighting probability begins to decline. The number of observations in the proximal strip where sighting probability is assumed to equal 1.0

is taken as an estimate of the true density of the target organism. A coefficient of detectability (CD) is calculated using the equation:

$$CD = n_1 * (W_2 / (n_2 * W_1)); \quad (3)$$

where W_1 = outer boundary width, W_2 = width of area in which sighting probability is assumed to equal 1.0, n_1 = total number of organisms sighted, n_2 = number of sightings in W_2 . The density of organisms in new areas is then:

$$D = n / (2 * L * W_1 * CD); \quad (4)$$

where n = the number of sightings in the area where density is to be estimated, and L = length of line snorkeled.

For my calculations, a cumulative frequency plot (cfp) of cumulative number of detections versus strip width was constructed. W_2 and n_2 were obtained by determining the line through the origin that was tangent to the cfp, then setting W_2 and n_2 equal to the strip width and cumulative number of detections, respectively, at the point where that line was tangent to the cfp (equivalent to the distance where probability of sighting no longer equals 1.0). The outer boundary width (W_1) was set equal to the width corresponding to the 95th percentile for the sighting distances. As with the Burnham estimates of $f(0)$, individual CD values were calculated for each turbidity level for each species.

Densities also were calculated using a strip transect model. For each site, strip width was set equal to twice the maximum visibility on the day of sampling, as determined either by Secchi disk extinction or turbidity level. The length of line snorkeled was multiplied by the strip width to estimate the area sampled. The number of sightings for each species was divided by the area sampled to obtain the density estimate for that species and site.

Densities for the electrofishing samples were calculated by multiplying the number of quadrats shocked at each site by 40 m², giving the total area sampled. The number of each species collected from all quadrats was divided by the total area

sampled to obtain an estimate of the number of each species per unit area. For convenience in comparison, all densities were expressed as number of fish per hectare (no./ha).

Statistical Analysis

For each species and turbidity level, a frequency distribution and box plot of sighting distances was visually inspected for agreement with assumptions of the strip transect approach typically used in underwater observation studies (i.e. that sighting probability is 1.0 out to the limits of observer visibility). Although no formal statistical tests were performed, gross violations of the equal sighting probability assumption should be apparent using this exploratory approach.

Kendall's tau was used to test for correlation, and paired t-tests were used to test for significant differences between density estimates for each species and estimation method. The functional relationship between individual pairs of estimation techniques was estimated using Theil-Sen non-parametric regression (Hollander and Wolfe 1973).

Results

Sighting distances

For all combinations of species and turbidity levels, there was evidence that the number of sightings decreased with increased distance of objects from the observer's line of travel. For the Roanoke darter, the number of observations increased slightly in the first 30 cm from the transect line and then declined out to point of maximum visibility at all turbidity levels (Figure 1.3). Values for the median, 75%, 90%, and 95% quantiles for sighting distance all declined with increasing turbidity (Figure 1.4). The 95% quantiles (equal to the boundary width for the Emlen estimates) under low, moderate, and high turbidity conditions were 133 cm, 104 cm, and 89 cm, respectively.

For the Roanoke logperch under low turbidity conditions, the number of

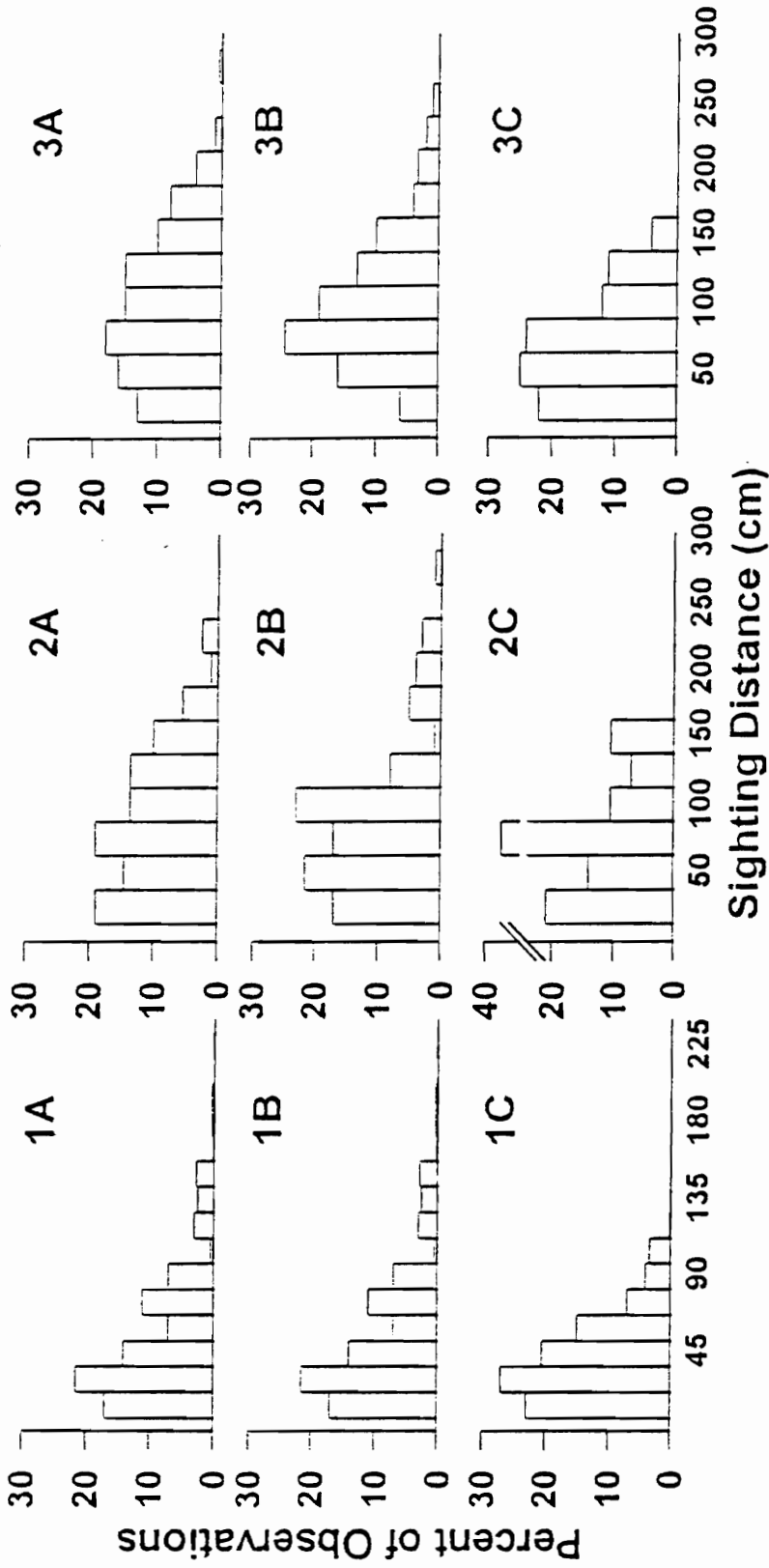


Figure 1.3. Frequency distributions of perpendicular sighting distances for Roanoke darter (graphs 1A-1C), Roanoke logperch (graphs 2A-2C), and black jumprock (graphs 3A-3C) under low turbidity (graphs 1A-3A, NTU < 3.5), moderate turbidity (graphs 1B-3B, NTU > = 3.5 and < 5), and high turbidity (graphs 1C-3C, NTU > = 5) conditions. Note the break in the y-axis for graph 2C.

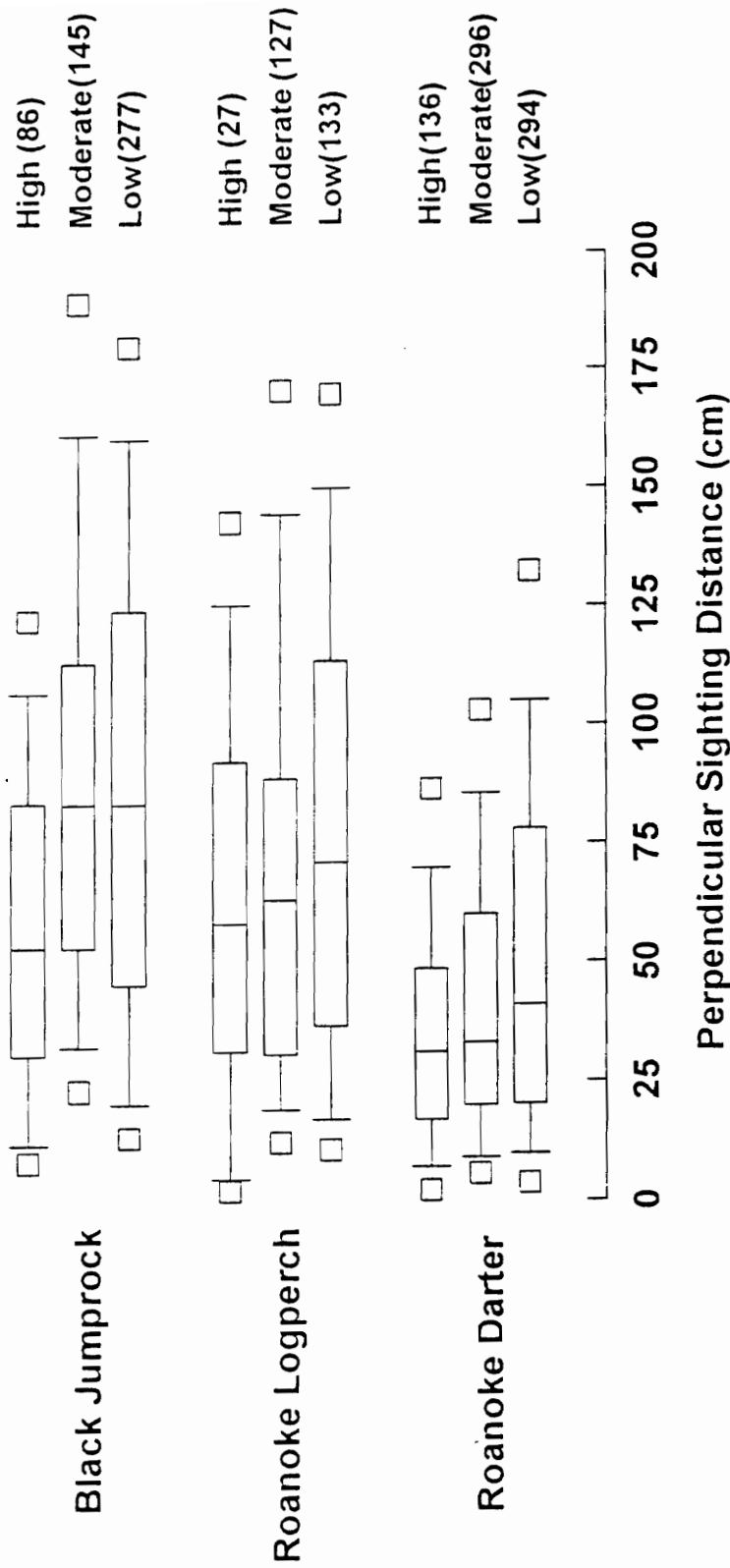


Figure 1.4. Box plots for Roanoke darter, Roanoke logperch, and black jumprock under low (NTU < 3.5), moderate (NTU >= 3.5 and < 5.0), and high (NTU > 5.0) turbidity conditions. The box encloses the middle 50% of the observations, the capped lines to the left and right of the box represent the 10% and 90% quantile, respectively, the squares to the left and right of the capped bars represent the 5% and 95% quantile, respectively, and the solid vertical bar in the box represents the median. Sample sizes are given in parentheses.

observations remained relatively stable out to a distance of 75 cm and then began to decline (Figure 1.3). Under moderate turbidity levels, the number of sightings remained stable or increased slightly out to a distance of 100 cm and then began to decline. Under high turbidity conditions, sightings increased out to 75 cm and then began to decline. Although values for median, 75%, 90%, and 95% quantiles generally declined as turbidity increased, there were two exceptions (Figure 1.4). The 95% quantile at low turbidity levels was slightly lower than that at moderate turbidity levels and the 75% quantile at moderate turbidity levels was lower than that at high turbidity levels. The 95% quantiles were 172 cm, 184 cm, and 142 cm for low, moderate, and high turbidity levels, respectively. The high turbidity results should be interpreted cautiously given the small sample size ($n=27$).

For the black jumprock under low turbidity conditions, there was a gradual increase in sightings out to a distance of 75 cm, followed by a decline (Figure 1.3). Under moderate turbidity conditions, sightings near the baseline were limited and there was a marked increase in the number of sightings out to approximately 75 cm, again followed by a decline in the number of sightings. At high turbidity levels, sightings remained stable or increased only slightly out to 75 cm, then declined rapidly. As with the logperch, median and 90% quantile declined as turbidity increased (Figure 1.4). The 75% quantile for sighting distance at moderate turbidity was slightly lower than at high turbidity while the 95% quantile at low turbidity was slightly lower than at moderate turbidity. The 95% quantiles were 181 cm, 188 cm, and 121 cm for low, moderate, and high turbidity levels, respectively.

Estimator comparisons

For the Roanoke darter, the paired *t*-tests revealed significant differences between all but two pairs of estimation techniques. The Burnham estimates did not differ significantly from the Emlen estimates ($P > .05$) and the quadrat estimates

did not differ significantly from the strip transect estimates ($P > .05$, Table 1.1). The correlation between the quadrat and strip transect estimates were significant ($P < .05$) while correlations between all other pairs of estimates were highly significant ($P < .01$, Table 1.1). Slopes of the Theil-Sen regressions indicated a one-to-one relationship between the Burnham and Emlen estimates, while the quadrat estimates were 66% lower and the strip transect estimates 73% lower than both the Burnham and Emlen estimates (Table 1.1). All of the Emlen estimates fell within the Burnham estimate 95% confidence intervals, while only five of the quadrat estimates and one of the strip transect estimates were contained within those same intervals (Table 1.2).

For the Roanoke logperch, paired t -tests showed the strip transect estimates were significantly different from Burnham ($P = .004$), Emlen ($P = .007$), and quadrat ($P = .021$) estimates, while all other pairs of estimates were not significantly different ($P > .05$, Table 1.3). Correlations between the three underwater observation estimation methods were all highly significant ($P < .01$), while correlations between the underwater observation estimates and the electroshocking estimates were significant ($P < .05$, Table 1.3). Slopes of the Theil-Sen regressions indicated that the strip transect estimates were 67%, 60%, and 60% lower than the Emlen, Burnham, and quadrat estimates, respectively, while the quadrat estimates were 40% and 55% lower than Burnham and Emlen estimates, respectively (Table 1.3). The slope of the Emlen-Burnham regression line indicated the Emlen estimates were 17% higher than the Burnham estimates (Table 1.3). As with the Roanoke darter estimates, all of the Roanoke logperch Emlen estimates fell within the 95% confidence intervals for the Burnham estimates (Table 1.4). Only 10 of 14 quadrat estimates and seven of 14 strip transect estimates fell within the Burnham confidence intervals.

The paired t -tests showed significant differences between the strip transect

Table 1.1 Results of Theil-Sen regressions, correlations (Kendall's Tau, and paired t-tests for comparisons among Burnham, Emlen, quadrat, and strip transect density estimates for the Roanoke darter. For paired t-tests, value is estimated mean difference between the first and second member of each pair. Significance levels for Kendall's Tau and t-tests are given in parentheses. NS indicates $P > 0.05$.

Estimators Compared	Regression Equation	Kendall's Tau	Estimated Difference
Burnham - Emlen	$Emlen = 0.99 \cdot Burnham + 32.93$	0.956 (<.001)	26.4 (NS)
Burnham - Quadrat	$Quadrat = 0.27 \cdot Burnham + 152.01$	0.604 (.003)	549.1 (.007)
Burnham - Strip	$Strip = 0.34 \cdot Burnham - 25.09$	0.692 (<.001)	657.2 (<.001)
Emlen - Quadrat	$Quadrat = 0.27 \cdot Emlen + 142.66$	0.604 (.003)	575.4 (.005)
Emlen - Strip	$Strip = 0.34 \cdot Emlen - 31.79$	0.692 (<.001)	683.6 (<.001)
Quadrat - Strip	$Strip = 0.59 \cdot Quadrat + 11.21$	0.589 (.019)	108.2 (NS)

Table 1.2. Abundance estimates (#/ha) for Roanoke darter from Roanoke River sites sampled during 1991 (RR1 - RR5) and South Fork Roanoke sites sampled during 1992 (SF1 - SF9). For the Burnham estimates, confidence intervals are given in parentheses.

Site	Burnham Estimate	Emlen Estimate	Strip Transect Estimate	Quadrat Estimate
RR1	1770.1 (1144.1 - 2738.7)	1725.9	660.1	1308.0
RR2	2318.8 (1511.6 - 3541.7)	2154.8	1164.0	650.0
RR3	1651.0 (1097.8 - 2483.1)	1609.8	759.1	550.0
RR4	1739.5 (1194.9 - 2532.4)	1929.6	370.4	230.0
RR5	914.0 (598.8 - 1466.2)	1013.9	835.7	593.0
SF1	2359.9 (1845.1 - 3002.5)	2430.0	760.0	700.0
SF2	574.7 (405.3 - 814.7)	566.7	97.0	263.0
SF3	276.0 (180.1 - 423.1)	306.2	47.6	306.0
SF4	571.7 (396.4 - 824.5)	645.1	121.9	388.0
SF5	262.9 (151.3 - 457.1)	244.9	48.7	28.0
SF6	98.9 (50.4 - 194.2)	96.4	24.3	63.0
SF7	78.9 (41.6 - 149.4)	92.3	23.1	100.0
SF8	415.5 (259.0 - 666.5)	501.5	87.3	464.0
SF9	719.8 (457.2 - 1133.3)	798.5	81.6	417.0

Table 1.3. Results of Theil-Sen regressions, correlations (Kendall's Tau), and paired t-tests for comparisons among Burnham, Emlen, quadrat, and strip transect density estimates for the Roanoke logperch. For paired t-tests, value is estimated mean difference between the first and second member of each pair. Significance levels for Kendall's Tau and t-tests are given in parentheses. NS indicates $P > 0.05$.

Estimators Compared	Regression Equation	Kendall's Tau	Estimated Difference
Burnham - Emlen	$Emlen = 1.17 \cdot Burnham - 3.30$	0.934 (<.001)	5.7 (NS)
Burnham - Quadrat	$Quadrat = 0.61 \cdot Burnham + 13.19$	0.508 (.012)	9.1 (NS)
Burnham - Strip	$Strip = 0.39 \cdot Burnham + 3.42$	0.780 (<.001)	29.5 (.004)
Emlen - Quadrat	$Quadrat = 0.45 \cdot Emlen + 19.20$	0.508 (.012)	14.8 (NS)
Emlen - Strip	$Strip = 0.33 \cdot Emlen + 5.70$	0.758 (<.001)	35.1 (.007)
Quadrat - Strip	$Strip = 0.41 \cdot Quadrat + 3.81$	0.464 (.021)	20.4 (.021)

Table 1.4. Abundance estimates (#/ha) for Roanoke logperch from Roanoke River sites sampled during 1991 (RR1 - RR5) and South Fork Roanoke sites sampled during 1992 (SF1 - SF9). For the Burnham estimates, confidence intervals are given in parentheses.

Site	Burnham Estimate	Enlen Estimate	Strip Transect Estimate	Quadrat Estimate
RR1	60.6 (28.2 - 130.1)	54.8	33.4	66.7
RR2	21.7 (10.5 - 44.8)	10.9	20.9	41.9
RR3	78.5 (46.0 - 133.9)	70.9	39.1	8.3
RR4	128.2 (79.3--207.1)	150.6	48.5	90.0
RR5	74.4 (42.9 - 129.4)	87.4	87.5	28.6
SF1	114.2 (66.2 - 196.9)	127.5	63.8	125.0
SF2	24.2 (9.1 - 54.2)	23.4	6.0	65.8
SF3	61.8 (30.9 - 123.9)	72.6	19.3	69.4
SF4	163.7 (94.1 - 284.7)	192.3	62.0	62.5
SF5	16.4 (3.7 - 72.9)	15.9	5.7	41.7
SF6	3.4 (0.4 - 26.4)	3.0	1.5	0.0
SF7	2.4 (0.3 - 19.0)	2.8	1.2	12.5
SF8	18.0 (5.1 - 63.9)	21.2	3.1	17.9
SF9	3.6 (0.5 - 28.2)	4.2	0.7	13.9

estimates and the Burnham ($P = .004$), Emlen ($P = .007$), and quadrat ($P = .025$) estimates for the black jumprock, while all other pairs of comparisons were non-significant ($P > .05$, Table 1.5). Kendall's correlation coefficients indicated highly significant ($P < .01$) correlations between Burnham and Emlen estimates, between Burnham and strip transect estimates, between Emlen and strip transect estimates, and between the strip transect and quadrat estimates (Table 1.5). The correlations between the quadrat estimates and the Burnham and Emlen estimates were significant ($P < .05$, Table 1.5). Slopes of the Theil-Sen regressions indicated that the Burnham and Emlen estimates were equivalent (Table 1.5). The quadrat estimates were 25% lower than the Burnham estimates and 33% lower than the Emlen estimates, while the strip transect estimates were 77%, 62%, and 59% lower than the Emlen, Burnham, and quadrat estimates, respectively, as indicated by the Theil-Sen slopes (Table 1.5). The Emlen estimates were contained within the Burnham estimate 95% confidence intervals for all 13 sites, while the strip transect and quadrat estimates were within those same intervals at only 7 of the 13 sites (Table 1.6).

Discussion

Adequacy of the strip transect sighting model

The frequency distributions for the perpendicular sighting distance data sets indicate that distance sampling models that assume decreased sighting probability with increased distance of the target from the line of travel provide a more appropriate conceptual approach for abundance estimation of benthic riffle fishes than strip transect methods. For the Roanoke darter and Roanoke logperch, the frequency of sightings generally declined as a function of increased sighting distance. For the black jumprock, the general pattern was an initial increase in frequency of sightings, followed by a decline as distance from the line increased. If the basic assumption for a strip transect sighting model had been met, the frequency distributions should have

Table 1.5. Results of Theil-Sen regressions, correlations (Kendall's Tau), and paired t-tests for comparisons among Burnham, Emlen, quadrat, and strip transect density estimates for the black juncrock. For paired t-tests, value is estimated mean difference between the first and second member of each pair. Significance levels for Kendall's Tau and t-tests are given in parentheses. NS indicates $P > 0.05$.

Estimators Compared	Regression Equation	Kendall's Tau	Estimated Difference
Burnham - Emlen	$Emlen = 0.98 \cdot Burnham - 0.81$	1.000 (<.001)	4.3 (NS)
Burnham - Quadrat	$Quadrat = 0.75 \cdot Burnham + 46.25$	0.487 (.020)	57.7 (NS)
Burnham - Strip	$Strip = 0.38 \cdot Burnham + 14.56$	0.590 (.005)	72.3 (.004)
Emlen - Quadrat	$Quadrat = 0.77 \cdot Emlen + 40.19$	0.487 (.020)	62.1 (NS)
Emlen - Strip	$Strip = 0.33 \cdot Emlen + 5.70$	0.590 (.005)	68.0 (.007)
Quadrat - Strip	$Strip = 0.41 \cdot Quadrat + 3.81$	0.590 (.005)	130.1 (.025)

Table 1.6. Abundance estimates (#/ha) for black jumprock from Roanoke River sites sampled during 1991 (RR1 - RR3, RR5) and South Fork Roanoke sites sampled during 1992 (SF1 - SF9). For the Burnham estimates, confidence intervals are given in parentheses.

Site	Burnham Estimate	Emlen Estimate	Strip Transect Estimate	Quadrat Estimate
RR1	271.8 (232.5-595.4)	335.7	302.5	583.3
RR2	122.5 (79.1-189.8)	111.4	108.0	758.3
RR3	140.3 (86.7 - 227.1)	126.7	140.3	75.0
RR5	214.9 (151.4-305.1)	223.5	115.4	228.6
SF1	66.3 (35.8 - 122.4)	86.1	52.1	178.0
SF2	109.3 (65.7 - 181.8)	99.4	35.0	92.1
SF3	241.9 (164.5 - 355.9)	237.7	74.8	305.6
SF4	252.9 (162.2 - 394.4)	248.5	95.0	125.0
SF5	24.0 (6.7 - 85.8)	21.8	7.6	13.9
SF6	7.9 (1.9 - 32.9)	7.2	4.6	25.0
SF7	4.9 (0.9 - 25.1)	4.8	2.4	62.5
SF8	190.9 (110.6 - 329.4)	187.5	33.0	89.3
SF9	260.5 (168.3 - 403.1)	261.3	54.0	222.2

been flat out to the maximum sighting distance, or at a minimum, for a significant portion of the total range of observations.

Further evidence that a strip transect sighting model is inappropriate for underwater estimation of benthic riffle fish density can be found in the box plots. The median value for sighting distance should be midway between the line of travel and maximum visibility distance. Making a conservative assumption that the 95% quantile for the sighting distance data sets equals the limit of visibility, then the median value is approximately 1/3 of the 95% quantile for each of the Roanoke darter data sets, and at approximately 2/5 of the 95% quantile for the Roanoke logperch and black jumprock data sets. Setting the limit of visibility equal to the Secchi disk extinction distance places the median value in the sighting data sets even further from the value expected under strip transect assumptions. The distribution of perpendicular sighting distances argues against use of uncorrected counts as density estimates for benthic riffle fishes. Furthermore, the significant differences between the strip transect estimates and the Burnham and Emlen estimates show that setting a strip width equal to maximum visibility results in a strong negative bias in density estimates.

Adequacy of line transect models

Three basic assumptions underlie valid line transect estimation; 1) objects on the line of travel are detected with certainty; 2) objects are detected at their initial location; and, 3) all measurements are exact (Buckland et al. 1993). Without ancillary data (i.e. an alternative manner of determining if fish on the line of travel are being missed), it is difficult to assess whether the first assumption is violated for the three species. Observations of fish behavior during the course of this study suggest that for the Roanoke logperch and black jumprock, this assumption is not violated. It is unlikely that a snorkeler could pass over an individual of either species without either seeing or disturbing (flushing) it. The interstitial spaces used by

logperch and jumprock are usually not large enough to completely obscure an individual. Furthermore, when individuals of either species were observed on the centerline, some type of flight response was nearly always initiated before the snorkeler passed over them. A similar response was observed for the Roanoke darter. However, many substrate interstices were large enough to obscure the darters, and some individuals may have taken cover and been overlooked. Density estimates for Roanoke darters may therefore be negatively biased, although the bias should be consistent across turbidity levels.

Gross violation of the second assumption (i.e. objects are detected at their original positions) results in frequency distributions with a peak in sightings well removed from the origin (Buckland et al. 1993). For the Roanoke logperch and Roanoke darter at all turbidity levels, there is only a slight increase in sightings for a short distance from the centerline (Figure 1.3). For the black jumprock, there is a substantial increase in sightings at moderate turbidity levels (Figure 1.3).

Behavior of the jumprock provides a possible explanation for the observed pattern. Based on personal observations, black jumprock have a "comfort zone" of somewhat more than 2.0 m. Once a snorkeler moved within 2.0 m, many jumprock exhibited a marked flight response. Under low turbidity conditions, it was often possible to observe individuals or groups just before or immediately following initiation of the flight response. Under moderate turbidity conditions, many observations were of individuals already in motion. Black jumprock moving directly along the line of travel probably remained beyond the snorkeler's field of vision, while those moving at an angle to the line of travel may have been observed at some distance from the transect line. Such movement patterns would result in the observed moderate turbidity frequency distribution. At high turbidity levels, observations were primarily of solitary individuals using crevices, boulders, and other substrate features as cover. Violation of the second assumption also results in a negative bias

in density estimates (Buckland et al. 1993). Due to differences in jumprock behavior under differing visibility conditions, the magnitude of the bias will not be consistent across visibility levels.

Given the manner in which data were collected in this study, the only likely source of error in measurement (assumption 3) would be if snorkelers moved off the transect line during the course of sampling. By moving off the transect line, an observer widens the area observed on one side of the line while narrowing it on the other. Although the distance between the line and any markers placed by the straying observer are still measured exactly, the perpendicular distances on the "wide side" are potentially beyond the observer's true field of vision and would result in inaccurate estimation of the sighting function. In order to minimize such violations, all personnel involved in data collection were fully informed of the importance of keeping the centerline of their body positioned over the transect line.

Line transect models are appropriate for estimation of Roanoke logperch densities, because there were no apparent gross violations of the three assumptions. For the Roanoke darter, the assumption that all individuals on the centerline were seen with certainty may have been violated. Because this problem should remain constant across turbidity levels, at worst the estimates obtained using the line transect model should provide a consistent index of abundance for this species. Line transect sighting models may not be appropriate for species such as the black jumprock, whose behavioral response to divers violated at least two of the original assumptions.

Comparisons among estimates

All of the statistical tests indicate that the Emlen and Burnham models performed equally well in estimating abundance of the three species. The strong positive correlations between the visual estimates and the electroshocking estimates for all three species suggest that at a minimum, underwater observation provides

estimates of relative abundance consistent at the ordinal level with the electroshocking technique. However, the quadrat estimates and the strip transect estimates were consistently lower than the Emlen and Burnham estimate across all three species. Wiley and Tsai (1983) estimated densities of a number of stream fishes using a backpack electroshocker and a three-pass depletion estimator. First pass recoveries for tessellated darter (Etheostoma olmsteadi) and white sucker (Catostomus commersoni), two species similar in size and behavior to the Roanoke darter and black jumprock, were 36% and 67% of their final density estimates, respectively. Because these values are very similar to the slopes of the quadrat - Burnham/Emlen regressions, underwater estimates for these two species would seem to be reasonably accurate. Unfortunately, because Wiley and Tsai (1983) did not sample a species with size and behavior similar to that of Roanoke logperch, no inferences can be drawn about the accuracy of the visual estimates for this species.

Conclusions

The simple Emlen model gave results similar to the more powerful Burnham model for all three species. Given the similarities in estimates, technique selection can be based on logistic considerations. With the Emlen model, once a correction factor is developed for a given species and environmental factor (i.e. turbidity level), it is unnecessary to obtain individual measurements on perpendicular distances. The only information needed to estimate abundance is the distance snorkeled, the number of fish seen, and the value of the environmental factor that determines the appropriate correction factor. The Burnham model requires information on the distribution of perpendicular sighting distances at each site for which an abundance estimate is needed. For fish biologists working with rare species, obtaining the number of observations needed for the Burnham model will often be impractical.

Once correction factors have been developed, the Emlen model lends itself well to studies designed to determine the distribution and abundance of benthic riffle

fishes. To adequately assess fish populations, sampling should be extensive rather than intensive (Hankin and Reeves 1988, Matthews 1990), covering as many sites as possible. Based on my experience, it is possible to do two replicate passes on five to six 150 m riffle/run sequences in a single day. At that rate of sampling, reach and watershed level estimates of species distribution and abundance become possible.

Despite the positive aspects associated with the Emlen model, it is also important to note its limitations. As mentioned earlier, conceptually simple sighting models achieve their simplicity at a cost of restrictive assumptions about the shape of the sighting function. The similarity between the Emlen and Burnham estimates may be a fortuitous agreement between the two sets of sighting functions for the species and sighting conditions I encountered rather than representative of a broader pattern common to all benthic riffle fishes. Until additional comparative studies of the relationship between competing sighting models are available, inferring that models with restrictive assumptions about sighting function form (e.g. the Emlen model) will perform as well as the more flexible models (e.g. the Burnham model) is ill-advised. Furthermore, the lack of statistical techniques to estimate the variance of estimates obtained with the simpler sighting models could be a serious shortcoming, particularly if no other estimation techniques are used that provide estimates of the precision of abundance estimates.

The larger class of distance sampling models discussed by Buckland et al. (1993) (of which the Burnham model is just one example) has proven to be both accurate and precise in situations where population densities were known with certainty and all assumptions were met (Burnham et al. 1980, Bergstedt and Anderson 1990). Thus, one approach for routine density estimation is to assume that estimates obtained with these models reflect true population densities and use these to "calibrate" estimates obtained with one of the conceptually simpler models. The simpler model could then be used to routinely estimate densities. This is essentially

the approach of Hankin and Reeves (1988) where three-pass depletion estimates were used to calibrate underwater counts of salmonids in streams in the Pacific Northwest.

The two line transect models I used represent a subset of the techniques available to fish biologists interested in using underwater observation. Additional research will no doubt reveal other models appropriate for situations different from this study. For target species other than open-water forms (e.g. salmonids, cyprinids) I strongly recommend models that incorporate factors correcting the number of fish observed for the probability of sighting. I also urge additional comparative studies where alternative estimation techniques are used to assess the precision and accuracy of underwater estimates.

CHAPTER 2

Microhabitat Suitability as an Indicator of Benthic Fish Abundance in Riffles

Introduction

As I indicated in the introduction to the dissertation, the most common habitat models used by stream fish biologists and managers are those relating the distribution and abundance of stream fish to some measure of the availability of preferred microhabitat in a reach of flowing water (Fausch et al. 1988, Stalnaker et al. 1995). Although the term microhabitat means different things to different people, the most widely accepted definition for stream fish uses water depth, water velocity, substrate type, and sometimes cover to describe habitat conditions in the immediate vicinity (a spatial scale of 10^{-1} to 10^2 m²) of the fish (Frissell et al. 1986, Bain and Finn 1991). The focus on these variables and the fine spatial scale stems both from results of ecological studies of habitat utilization by stream fish and practical management considerations.

Ecological studies show that stream fish show marked species segregation along depth, velocity, substrate, and cover axes (Gorman and Karr 1978, Fausch and White 1981, Grossman et al. 1987). This partitioning of physical space has been taken as evidence that differential use of these variables has adaptive significance and is therefore an important factor determining the distribution and abundance of stream fish (Matthews et al. 1982, Ross 1986, Harvey 1991). From a practical standpoint, many anthropogenic impacts involve alteration of both the volume of water passing through the stream channel and the temporal distribution of flow fluctuations (Bain and Boltz 1989, Benke 1990, Stalnaker et al. 1995). Obviously such flow alterations will change the spatial and temporal availability of depth and

velocity and to a lesser degree, substrate and cover in lotic waters. Given that these habitat characteristics have adaptive significance for stream fish, management of flow regimes is a concern for managers of stream fish resources.

Although stream habitat management models utilizing univariate microhabitat descriptors (e. g. the Physical Habitat Simulation [PHABSIM] module of the Instream Flow Incremental Methodology [IFIM] developed by the U. S. Fish and Wildlife Service) are sometimes successful in the salmonid systems in which they were developed (Nehring and Anderson 1993, Stalnaker et al. 1995), this success declines when they are applied to the taxa-rich streams in other parts of the country (Leonard and Orth 1988, Bain and Boltz 1991). A number of hypotheses have been advanced to explain the diminished capacity of microhabitat availability to predict changes in fish abundance with shifts in habitat characteristics. These include (but are not limited to) the presumably increased importance of biotic interactions in systems with higher species richness, angler harvest, variability in the temporal and spatial characteristics of habitat use by stream fish, failure of univariate habitat variables to identify fish response to interactions among variables, and failure to identify limiting life stages (Mathur et al. 1984, Orth 1987, Gore and Nestler 1988).

My purpose in this chapter was not to address all the potential problems that have been identified for fine-scale microhabitat models, but to develop the most reasonable microhabitat models for the three study species given the constraints outlined in the introduction to the dissertation. Within those constraints, the factors that I could attempt to control for were variation in fish habitat use among reaches and response of the study species to interactions among the measured microhabitat variables.

In this study, I took an empirical approach to addressing whether fish respond to microhabitat characteristics independently or alternatively, if fish respond to interactions among microhabitat characteristics. The null hypothesis tested was

that there would be no difference between descriptions of microhabitat use developed using the two approaches. Given rejection of the first hypothesis, a second question addressed was whether a multivariate representation of microhabitat provided better predictions of fish abundance than a representation that assumed no interaction in fish response to microhabitat characteristics. The null hypothesis in this case was that there would be no difference in the ability of the two microhabitat models to predict fish abundance. I also used an empirical approach to look at differences in microhabitat use by Roanoke darter, Roanoke logperch and black jumprock between two spatially distinct reaches within the upper Roanoke River basin. The null hypothesis here was that there would be no differences in habitat use between the two reaches, with the alternative being that habitat use differed between reaches for the three species. Given resolution of these problems, the final step was to use the resulting microhabitat preference characterizations for the three species to predict their abundance.

To summarize, my study had two objectives: 1) to compare similarities and differences in late summer microhabitat use by the three target species using both univariate and multivariate descriptors of habitat characteristics, and 2) to determine the utility of late summer microhabitat availability as a predictor of the abundance of the three target species.

Methods

Study Site

Sites in two separate reaches of the upper Roanoke Basin were sampled in this study. During 1991, eight sites (referred to hereafter as RR1 - RR8) on the mainstem Roanoke River in Roanoke County, Virginia were sampled (Figure 2.1). In 1992 and 1993, an additional six sites (referred to hereafter as SF1 - SF 6) on South Fork Roanoke River in Montgomery and Roanoke counties, Virginia were

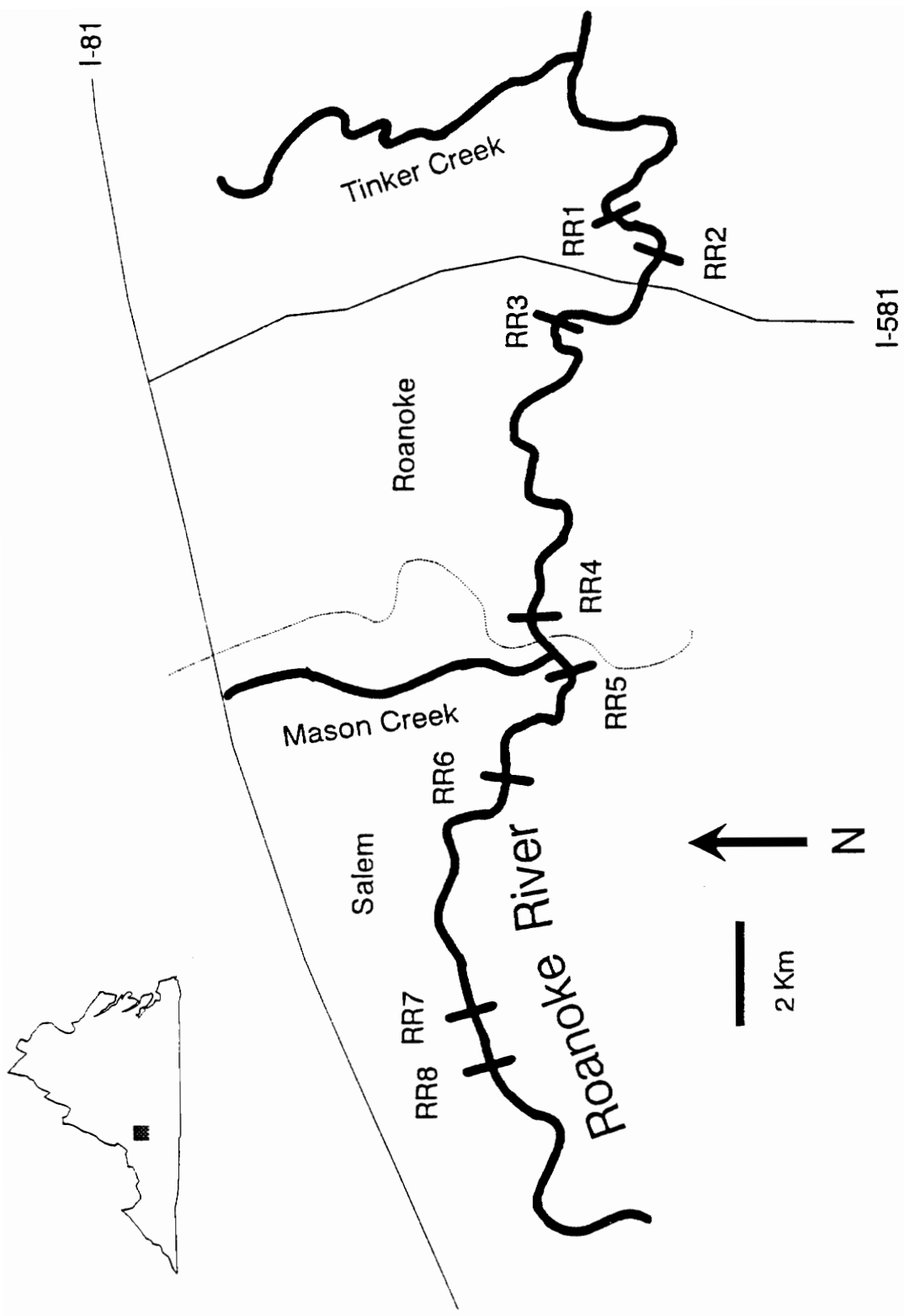


Figure 2.1. Study sites sampled during 1991 on Roanoke River in Roanoke County, Virginia.

sampled (Figure 2.2).

Microhabitat Use Quantification

Underwater observation was used to quantify microhabitat for Roanoke darter and Roanoke logperch at five sites on Roanoke River in 1991 (RR1, RR5 - RR8), for black jumprock at four sites on Roanoke River in 1991 (RR1, RR5, RR6, and RR8), and for all three species at all six sites on South Fork Roanoke River in 1992. All sites were sampled at low streamflow conditions during late summer or early fall. Techniques used were similar to those described in Chapter 1 for line transect density estimation. Snorkeling lines parallel to streamflow were marked using yellow cotton twine secured to the substrate with reinforced iron bars. Snorkelers entered the water at the downstream end of the site and moved slowly upstream along the marked lines. When one of the three target species was sighted, a species-specific colored marker was placed at the position where the fish was first observed. In some instances for some species, multiple passes were made through a site to obtain additional observations. Following completion of the snorkeling pass(es), the spatial location of each marker was quantified by recording the linear distance from the downstream end of the line and the perpendicular distance either to the right or left of the line. The spatial location of each line was referenced to a series of base points systematically located along either bank which were used to designate a cartesian coordinate system for each site. Combining the base points with the linear and perpendicular distances recorded for the fish positions allowed assignment of a unique x- and y-coordinate value in the cartesian coordinate plane for each observation.

After all underwater observation passes at a given site were completed, available habitat was quantified at transects spaced 15 m apart, perpendicular to water flow. At each of the transects, depth, velocity and substrate characteristics

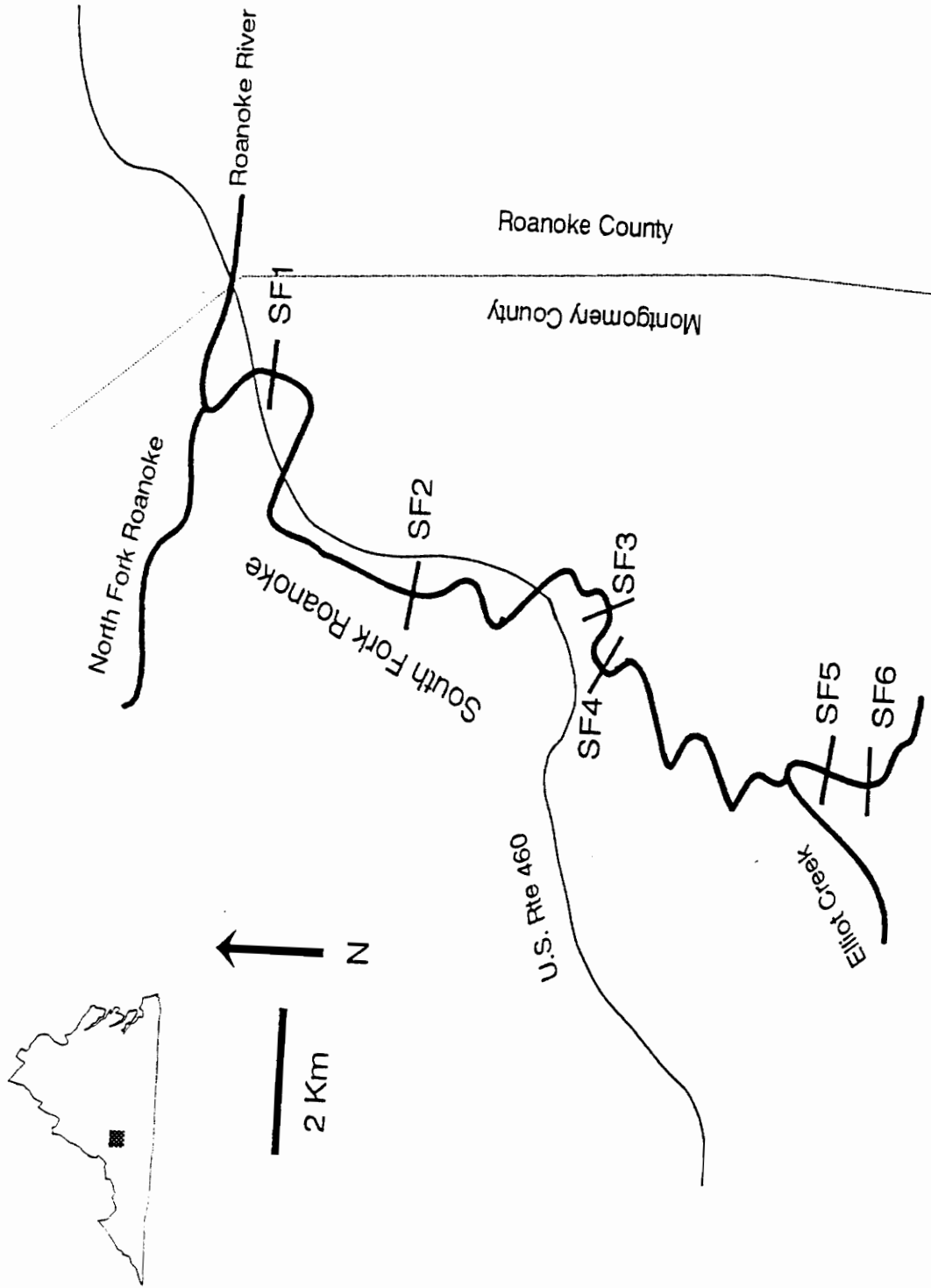


Figure 2.2. Study sites sampled during 1992 and 1993 on south Fork Roanoke River in Montgomery County, Virginia.

were recorded at a series of points located 3 m apart along the transect. The number of habitat points measured at each site ranged from 47 to 95. Water depth (cm) and mean water column velocity (cm/s) were measured, and primary and secondary substrate types and degree of siltation were visually estimated. Substrate was classified using a modified Wentworth scale with seven categories (Platts et al. 1983). The first six categories were based on particle size ranging from silt through boulder. The seventh category was bedrock. Siltation was assessed by visually estimating the proportion of the substrate and interstitial spaces covered with fine silt and clay particles. An ordinal rank was assigned ranging from 1 (all surfaces and interstitial spaces covered with fine particles) to 5 (less than 5% of the interstitial spaces covered with fine particles). The location of each of the transects was referenced to the base points along each of the banks, allowing assignment of a unique x- and y-coordinate to each of the measured habitat points in the previously described cartesian plane.

Abundance estimation

During 1991, abundance of the three species was estimated twice at all 8 sites on Roanoke River, once in late July or August and once in September or early October, using the quadrat-based electrofishing technique described in Chapter 1. During 1992 and 1993, abundance of the target species was estimated at all 6 sites on South Fork Roanoke in August or early September using the same technique. Following abundance estimation, habitat availability was quantified using the same technique described for the underwater observation habitat quantification in the previous section.

Development of Measures of Habitat Use

I quantified fish abundance in spatially discrete habitat cells. Using a cell-

based approach avoids problems of correcting habitat use by habitat availability (Cheslak and Garcia 1988, Rubin et al. 1991). I assumed that each of the measured habitat points represented the center of a rectangular cell 45 m² (3 m wide and 15 m long) whose boundaries were defined longitudinally as one-half the distance to the upstream and downstream habitat transects and laterally as one-half the distance to the left and right points along the same transect. I also assumed that values recorded at the cell's center adequately represented habitat conditions throughout that cell. Comparison of cell habitat variable values with habitat variable values collected at individual fish positions within each cell indicated this assumption was tenable (W. E. Ensign, unpublished data). Since each fish position was given a unique x- and y-coordinate, it was possible to estimate the density of fish in any sampled cell by summing the number of fish observed within that cell. To avoid weighting habitat at sites where multiple passes were made more heavily than those where only a single pass was made, the number of fish observed in a cell was divided by the total number of observation passes made at that site. Cells that were outside the area sampled during the course of underwater observation passes were not included in the data set.

Discrete class intervals were developed for each of the measured habitat variables. Depth and mean column velocity were divided into 10 cm and 10 cm/s intervals, respectively. Primary and secondary substrate were collapsed into a single, three-category measure of substrate coarseness (Table 2.1), and siltation was collapsed into a binary classification of silted (siltation ranking ≤ 3) versus unsilted (siltation ranking > 3). Fish densities were then estimated for each of the class intervals for all four habitat variables.

Multivariate habitat categories were developed by dividing depth into shallow (< 20 cm), moderate (≥ 20 cm and < 40 cm) and deep (≥ 40 cm) classes, velocity into slow (< 20 cm/s), moderate (≥ 20 cm/s and < 50 cm/s), and fast

Table 2.1. Classification table used in developing the three-category substrate roughness variable.

Secondary Substrate Type	Dominant Substrate Type						
	1	2	3	4	5	6	7
1	Fine	Fine	Fine	Moderate	Coarse	Coarse	Fine
2	Fine	Fine	Fine	Moderate	Coarse	Coarse	Fine
3	Fine	Fine	Fine	Moderate	Coarse	Coarse	Fine
4	Fine	Fine	Moderate	Moderate	Coarse	Coarse	Fine
5	Fine	Moderate	Moderate	Coarse	Coarse	Coarse	Moderate
6	Fine	Moderate	Moderate	Coarse	Coarse	Coarse	Moderate
7	Fine	Fine	Fine	Moderate	Coarse	Coarse	Fine

(> 50 cm/s) classes, and using the three-category and two-category classifications for substrate roughness and siltation, respectively. Combining all classes for all habitat measures resulted in 54 possible habitat combinations. Because of the interaction between depth, velocity, and substrate deposition characteristics, there are some combinations of variables that will not occur. For example, fine silted substrate in deep, fast water will probably never occur in most lotic systems. Furthermore, some habitat combinations occurred only rarely. To insure that all classes had some observations, some classes were lumped, resulting in a total of 21 distinct habitat combinations (Table 2.2). Darter, logperch, and jumprock densities were then estimated for each of the unique habitat configurations in the same manner as for the univariate habitat categories.

In addition to measures of habitat use for the combined data set, subsets of the data were also created for observations from the 1991 Roanoke River habitat observations and the 1992 South Fork Roanoke habitat observations. The three data sets will be referred to hereafter as the combined, Roanoke, and South Fork data sets.

Statistical Analysis

Development of microhabitat suitability models is based on the premise that fish use only a subset of the range of a given variable (Orth and Maughan 1982). In order to determine if there were differences in fish density among classes for the univariate variables (depth, velocity, substrate, and siltation), I used a Kruskal-Wallis test. For the multivariate habitat descriptor, the Kruskal-Wallis test was used to test for density differences among the 21 habitat combinations. Separate tests for differential habitat use were conducted for all three data sets and all three species. If the P-value for the test was less than 0.05, I took this as evidence that use differed among intervals for the univariate variables or among combinations for the

Table 2.2. Habitat combinations and number of cells sampled in the development of the multivariate suitability indices. The first number given is the total number of cells sampled, the second is the number of cells sampled in Roanoke River and the third is the number sampled in South Fork Roanoke. Depth classes are shallow (<20 cm), moderate (≥ 20 cm and <40 cm), and deep (≥ 40 cm). Velocity classes are slow (<20 cm/s), moderate (≥ 20 cm/s and < 50 cm/s), and fast (> 50 cm/s). Fine, moderate, and coarse substrate classes and silted versus unsilted conditions are as defined in the text.

Siltation	Depth	Velocity	Substrate Roughness	Roanoke Darter/ Roanoke Logperch	Black Jumprock
Silted	Shallow	All	All	26/15/11	25/14/11
Silted	Moderate	All	All	19/8/11	18/7/11
Silted	Deep	All	All	17/12/5	17/12/5
Unsilted	Shallow/ Deep	Slow/ Moderate	Fine	21/10/11	14/3/11
Unsilted	Shallow	Slow	Moderate	24/9/15	24/9/15
Unsilted	Shallow	Slow	Coarse	26/14/12	21/9/12
Unsilted	Shallow	Moderate	Moderate	22/8/14	22/8/14
Unsilted	Shallow	Moderate	Coarse	30/10/20	28/8/20
Unsilted	Shallow	Fast	All	14/8/6	14/8/6
Unsilted	Moderate	Slow	Fine	9/4/5	8/3/5
Unsilted	Moderate	Slow	Moderate	14/8/6	13/7/6
Unsilted	Moderate	Slow	Coarse	26/15/11	21/10/11
Unsilted	Moderate	Moderate	Fine	17/6/11	16/5/11
Unsilted	Moderate	Moderate	Moderate	40/22/18	38/20/18
Unsilted	Moderate	Moderate	Coarse	97/60/37	84/47/37
Unsilted	Moderate	Fast	All	54/29/25	50/25/25
Unsilted	Deep	Slow	Moderate	8/4/4	8/4/4
Unsilted	Deep	Slow	Coarse	11/3/8	10/2/8
Unsilted	Deep	Moderate	Moderate	17/9/8	16/8/8
Unsilted	Deep	Moderate	Coarse	35/21/14	30/16/14
Unsilted	Deep	Fast	All	15/7/8	11/3/8

multivariate classification.

Given differences in habitat utilization, the next step was to construct cell suitability indices using those variables showing evidence of differential use. For the univariate variables, I assumed that each of the variables showing significant differences in use was equally important in determining cell suitability and therefore should be given equal weighting in a cell suitability index. I accomplished this by dividing the mean fish density for a variable interval class by the maximum mean density for any interval within that variable. This scales each univariate variable from a minimum value of 0 (no fish observed in that interval) to 1 (maximum observed mean density for that variable). As an example, assume mean darter density in the 10-20 cm depth interval was 2 fish per cell, the maximum observed mean density was 10 fish per cell in the 50-60 cm interval, and no darters were seen in water less than 10 cm deep. The darter depth suitability index value for cells less than 10 cm deep would be 0, 0.2 for cells 10-20 cm deep, and 1.0 for cells 50-60 cm deep. Given individual suitability indices for each significant univariate variable, overall suitability of a given cell was estimated using the following equation:

$$\text{Cell Suitability} = (H_1 * H_2 * H_n)^{1/n}, \text{ where}$$

H_1 = the suitability value for habitat factor 1 (e. g. depth),

H_2 = the suitability value for habitat factor 2,

H_n = the suitability value for habitat factor n,

and n = the number of habitat factors used.

For the multivariate habitat descriptor, I used mean fish density observed in a given habitat combination as the cell suitability value. Univariate and multivariate cell suitability indices were developed for the combined, Roanoke River, and South Fork data sets for all three species.

The next step in the analysis was to determine whether cell suitability values

allowed me to predict the abundance of the three study species at the 28 sites where I had electroshocking estimates of fish abundance. One of the basic assumptions of habitat suitability models is that sites with higher overall suitability support higher densities of the target species than sites with lower overall suitability. The most common way to convert habitat specific suitability values to a measure of site quality (usually termed weighted usable area [WUA]) is to multiply each area of a given type of habitat by its suitability value and then sum the products across the site. Since all my habitat cells were of equal area, I simply summed the individual univariate and multivariate cell suitabilities to obtain a univariate and multivariate measure of WUA. In order to determine the transferability of the various suitability ratings, I estimated WUA for all 28 sites using suitability criteria developed from the combined, Roanoke River, and South Fork data sets. The ability of the two suitability indices to serve as predictors of the abundance of the three target species was determined by looking at the correlation between the WUA values and abundance estimates obtained using the quadrat-based electroshocking technique. Because data for estimation of fish habitat use and data for abundance estimation were collected from some of the same sites (five of the 16 Roanoke River sites and all six 1992 South Fork sites) the correlations are a relatively weak test of the predictive ability of the habitat suitability models. Since the relationship between abundance and habitat quality may not be linear, Spearman's rank correlation coefficient was used instead of Pearson's correlation coefficient.

The final step was to determine if univariate and multivariate suitability indices differed in their ability to identify suitable and unsuitable habitat types. Since the class intervals for the univariate and multivariate suitability indices developed for estimation of weighted usable area differed, they are not directly comparable. In order to circumvent this problem, I recalculated the univariate depth and velocity suitability indices using the multivariate depth and velocity categories and then

developed univariate cell suitabilities for each of the multivariate habitat combinations. For those combinations that lumped more than one habitat configuration into a single class (for example, at moderate depths over silt, the three substrate classes and three velocity classes were combined), I took the average of the individual univariate suitabilities making up that class. The multivariate and univariate indices were then ranked from highest suitability to lowest suitability and Spearman's correlation coefficient was used to determine concordance among ranks. As with the other portions of this study, these manipulations were carried out for all three data sets and all three species.

Results

Habitat Use

The Kruskal-Wallis tests indicated that there were significant differences in Roanoke darter cell densities for all four univariate habitat variables (depth, velocity, substrate, and siltation) for the combined, Roanoke, and South Fork data sets (Figure 2.3). Differences in darter densities among the multivariate habitat categories were also significant for all three data sets (Figure 2.4). With minor exceptions, there was generally good agreement between the types of habitat used by darters in the Roanoke and South Fork for both the univariate and multivariate habitat descriptors. The univariate distributions indicate greater use of deeper areas and fine substrate in the South Fork than in the Roanoke (Figure 2.3). The most noticeable difference in the multivariate habitat descriptors between reaches was the absence of darters in deep slow areas with moderate to coarse, unsilted substrates in the Roanoke and low to moderate densities in the same types of areas in the South Fork (Figure 2.4).

Roanoke logperch densities did not differ among substrate types for any of the three data sets or among depth intervals for the Roanoke data set, but differences in density were significant for all other univariate variables across data sets (Figure

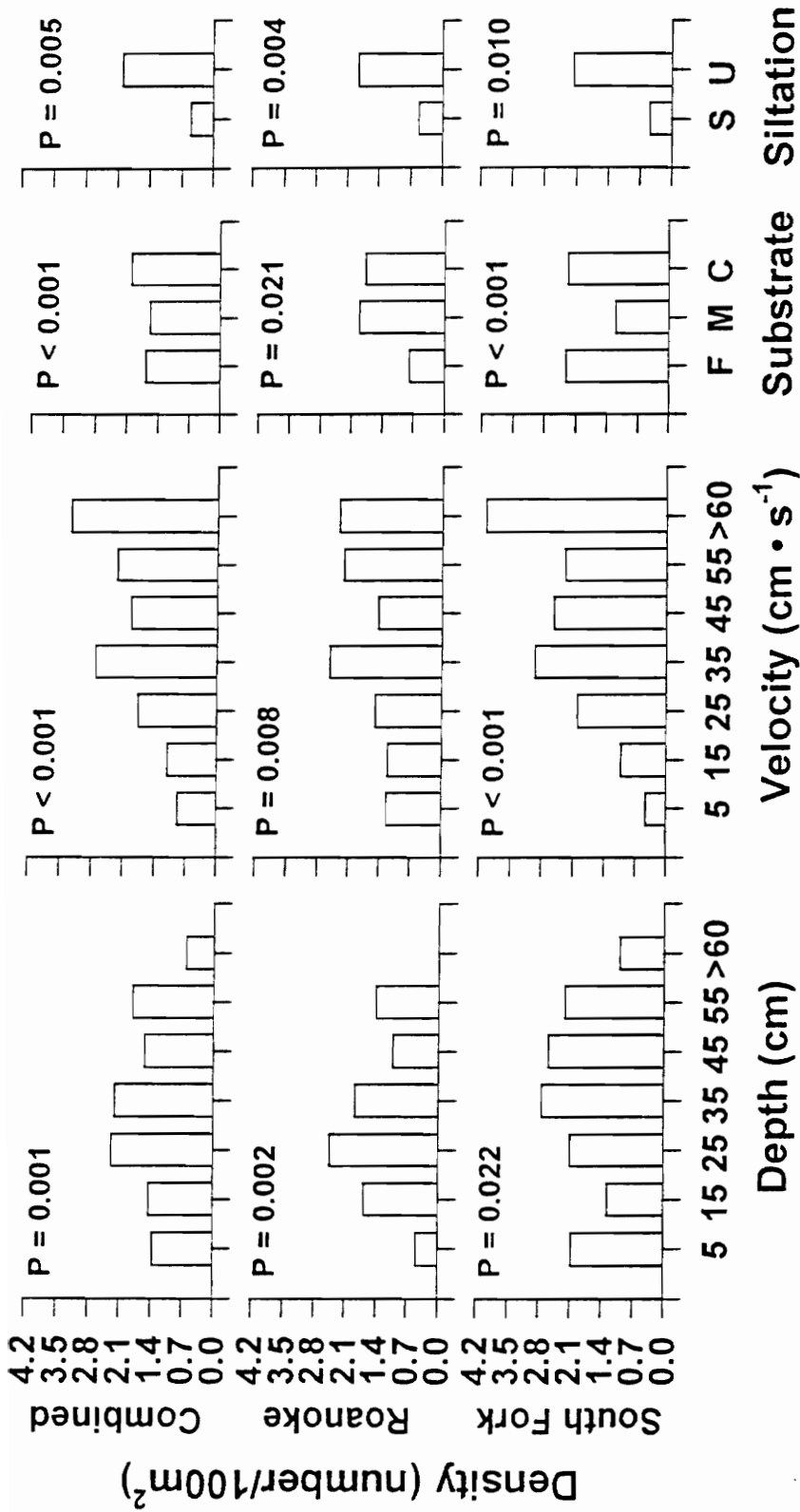


Figure 2.3. Densities (number per 100 m²) of Roanoke darter by class interval for depth, mean column velocity, substrate roughness, and level of siltation from the combined, Roanoke, and South Fork data sets. For depth and velocity, numbers on the ordinate represent interval mid-points. Abbreviations for substrate are F=fine, M=moderate, C=Coarse and for siltation are S=silted and U=unsilted. Significance levels of Kruskal-Wallis test for differences in median densities among intervals are given on each graph.

2.5). As with Roanoke darter, there were significant differences among multivariate habitat combinations for all three data sets (Figure 2.6). The most noticeable difference among data sets in the univariate habitat distributions was for depth: South Fork logperch were most abundant in moderate to deep water and virtually absent from shallow areas, while logperch density in the Roanoke was relatively uniform across depths (Figure 2.5). Differences in use of the multivariate habitat combinations was more evident. Logperch were absent from slow velocity water at shallow to moderate depths in the South Fork, while they appeared at low to moderate densities in similar habitats in the Roanoke. Conversely, logperch used habitat combinations containing deep water to a much greater degree in the South Fork than in the Roanoke (Figure 2.6).

Black jumprock showed significant differences for all univariate habitat variables with the exception of velocity in the South Fork data set and substrate in the Roanoke data set (Figure 2.7). Densities in the multivariate habitat combinations were significantly different for all three data sets (Figure 2.8). Differential habitat use between reaches was even more noticeable for jumprock than for either darter or logperch. Univariate use of depth in the South Fork was strongly skewed towards deeper water while Roanoke River jumprock occurred most commonly in moderate depths. Densities were markedly higher in fast water in the Roanoke but appeared to be uniform across velocities in the South Fork. Finally, jumprock densities were highest over coarse substrate in the South Fork but uniform across substrate types in the Roanoke data set (Figure 2.7). The South Fork multivariate data set showed that black jumprock were found almost exclusively in habitat combinations containing deep water, while the Roanoke data set indicate use of a broad range of habitat combinations. As with the logperch, jumprock were absent from deep slow areas in the Roanoke River, but unlike logperch, reached their highest densities in these habitats in the South Fork (Figure 2.8).

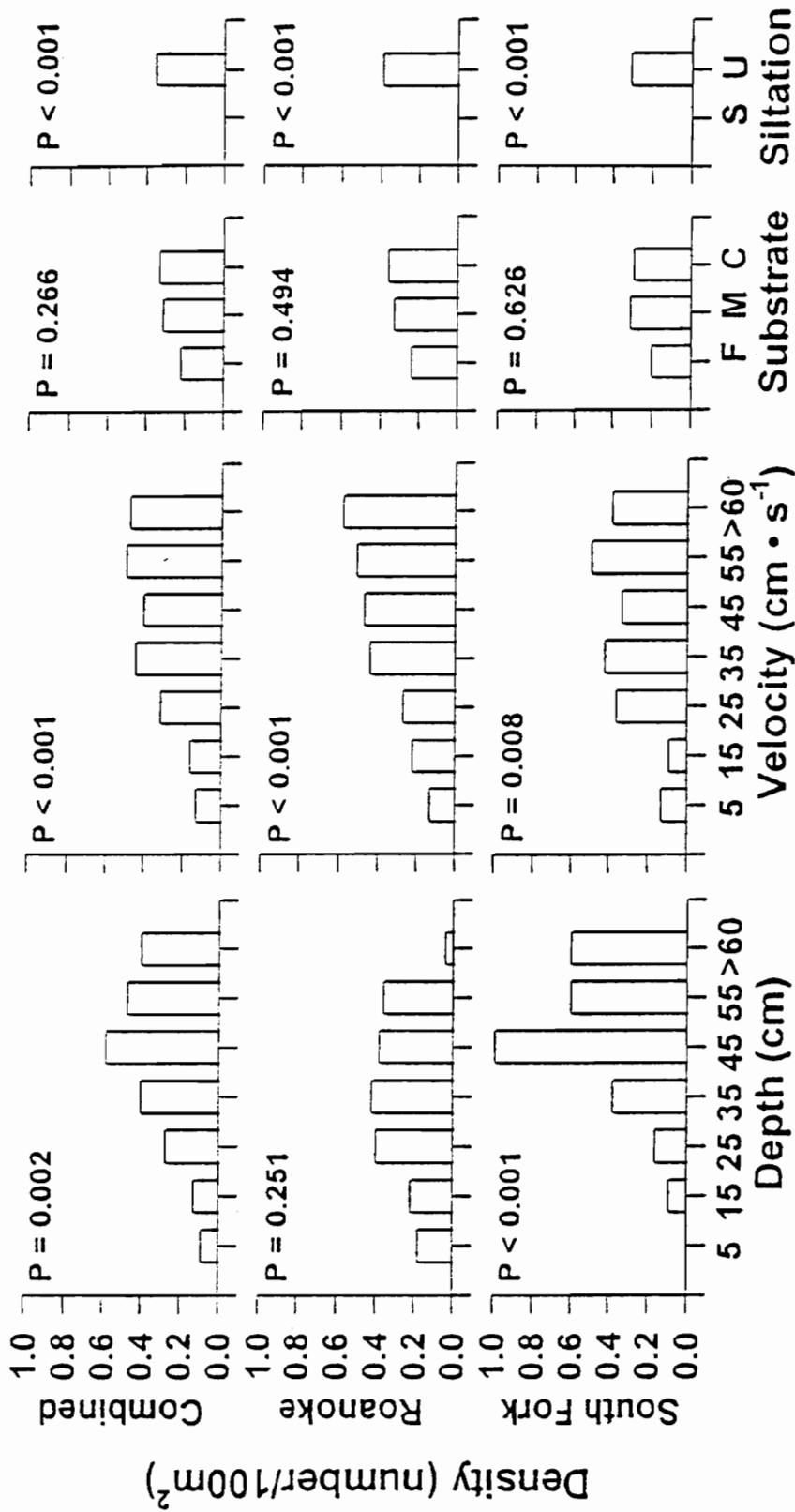


Figure 2.5. Densities (number per 100 m²) of Roanoke logperch by class interval for depth, mean column velocity, substrate roughness, and level of siltation from the combined, Roanoke, and South Fork data sets. For depth and velocity, numbers on the ordinate represent interval mid-points. Abbreviations for substrate are F=fine, M=moderate, C=Coarse and for siltation are S=silted and U=unsilted. Significance levels of Kruskal-Wallis test for differences in median densities among intervals are given on each graph.

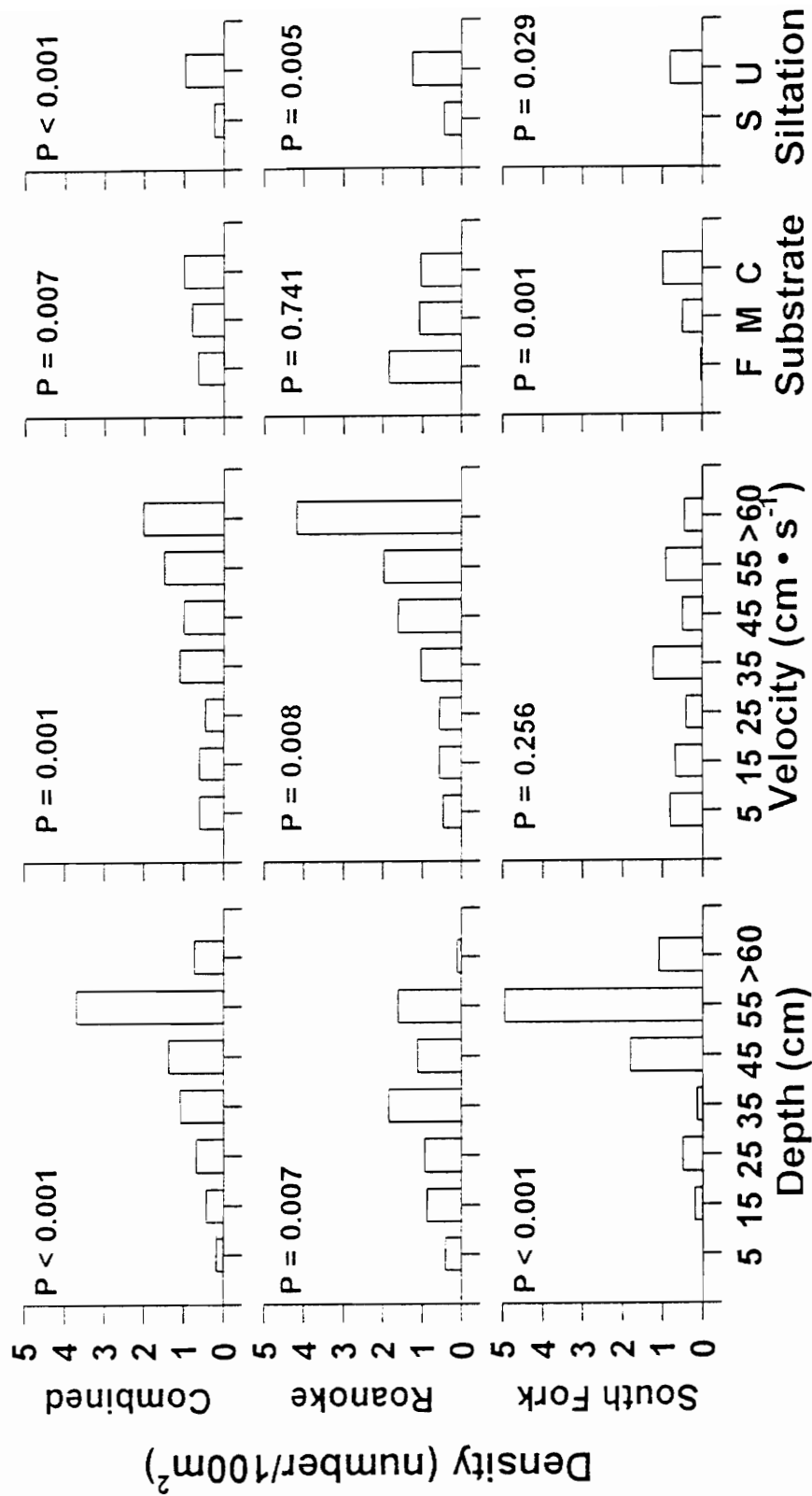


Figure 2.7. Densities (number per 100 m²) of black jumprock by class interval for depth, mean column velocity, substrate roughness, and level of siltation from the combined, Roanoke, and South Fork data sets. For depth and velocity, numbers on the ordinate represent interval mid-points. Abbreviations for substrate are F=fine, M=moderate, C=Coarse and for siltation are S=unsilted and U=unsilted. Significance levels of Kruskal-Wallis test for differences in median densities among intervals are given on each graph.

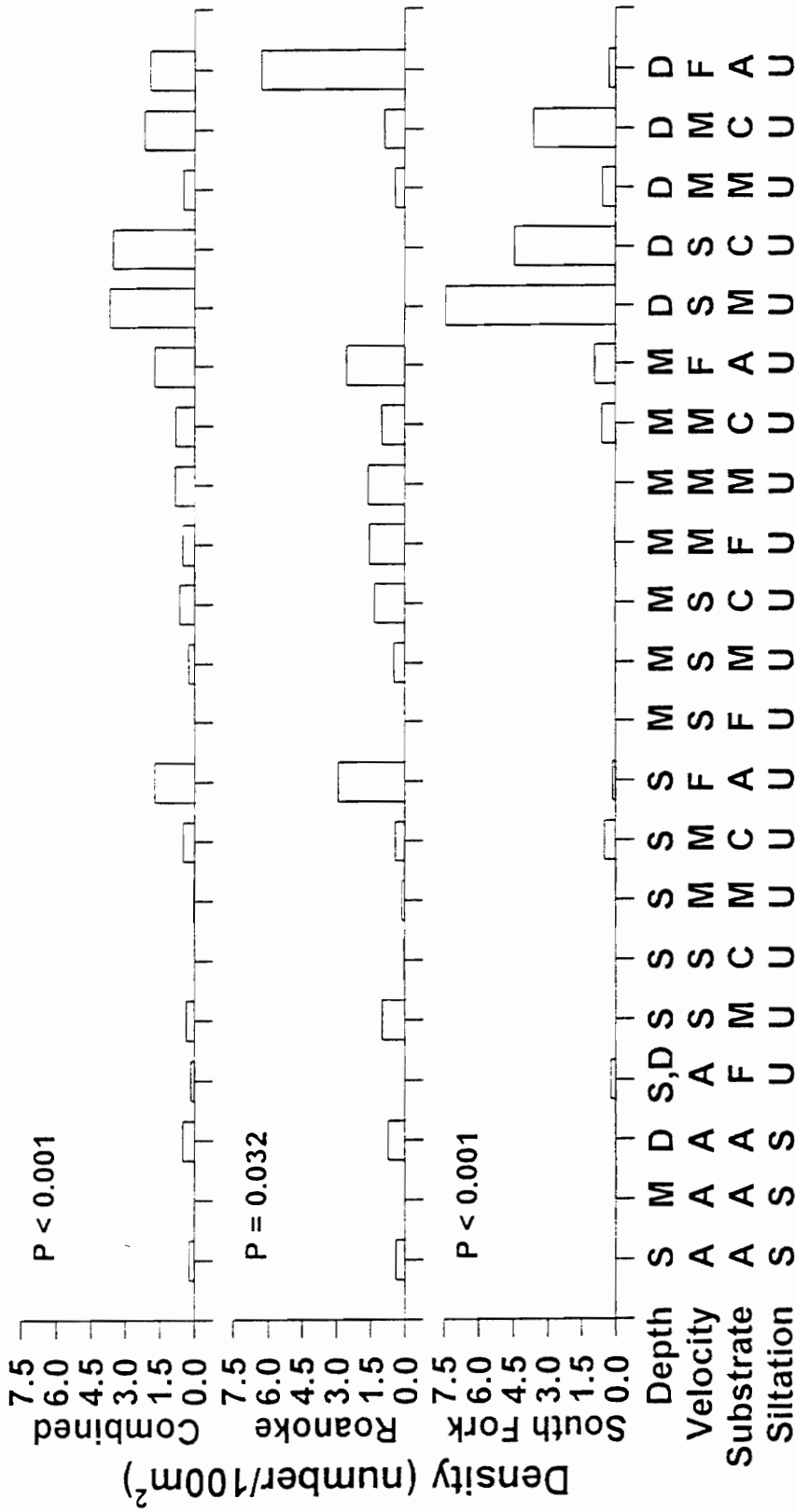


Figure 2.8. Densities (number per 100 m²) of black jumprock in each of the 21 multivariate habitat combinations from the combined, Roanoke, and South Fork data sets. Abbreviations on the ordinate for depth are S=shallow, M=moderate, and D=deep; for velocity S=slow, M=moderate, F=fast, A=all; for substrate F=fine, M=moderate, C=rough, A=all; for siltation S=silted, U=unsilted. Significance levels of Kruskal-Wallis test for differences in median densities among combinations are given on each graph.

In summary, both univariate and multivariate habitat descriptors provided strong evidence for differential use of habitat types in all of the data sets for Roanoke darter, Roanoke logperch, and black jumprock. Habitat use was relatively consistent across reaches for both univariate and multivariate habitat descriptors for the darter, but showed noticeable differences among reaches for the logperch and jumprock. All three species tended to use deeper water in the South Fork than in the Roanoke.

Comparison of Suitability Indices

Correlations between the recalculated univariate and multivariate suitability indices for all three species across all three data sets were highly significant (all $P < 0.01$, Figures 2.9, 2.10, and 2.11). For the Roanoke darter, the only gross differences in index rankings of the indices were for the shallow/deep, all velocity, unsilted substrate class and the moderate depth, slow velocity, fine unsilted substrate class in all three data sets (Figure 2.9). The first combination received high multivariate and low univariate ratings while the second combination received low multivariate and high univariate ratings. The only other difference of note was in the combined data set where the multivariate index ranked moderate depth, slow velocity water over moderate, unsilted substrate as highly suitable and the univariate index ranked the same combination low (Figure 2.9).

For logperch, there were no consistent differences in the multivariate and univariate rankings across all three data sets but there were minor differences within individual data sets (Figure 2.10). In both the combined and Roanoke data set shallow, slow cells with unsilted, moderate substrate received high multivariate and low univariate rankings while shallow, moderate velocity cells with unsilted, coarse substrate received low multivariate and high univariate rankings. The South Fork data set showed ranking differences for shallow, fast, unsilted cells over all substrate

types, and for slow velocity, moderate depth cells over unsilted, moderate substrates.

As with the Roanoke logperch, there were no consistent differences in index rankings across data sets for the black jumprock (Figure 2.11). Both the combined and Roanoke data sets showed differences in deep, silted cells across all substrates and velocities and in moderate depth, slow velocity cells over fine, unsilted substrates. The combined data set also showed differences in univariate and multivariate rankings for deep, moderate velocity, moderate substrate, unsilted cells. In addition to the two combinations already listed, the Roanoke data set showed differences in index rankings for shallow, slow, unsilted moderate substrate cells and moderate depth, slow, coarse unsilted substrate cells. Finally, differences in index rankings in the South Fork data set occurred in the shallow/deep, all velocity, fine unsilted substrate cells and in slow, moderate depth and substrate, unsilted cells. In summary, there was little evidence for differences in suitability due to failure to include interactions among habitat variables.

Abundance - Weighted Usable Area Correlations

Correlations between abundance of Roanoke darter, Roanoke logperch, and black jumprock and weighted usable area estimates based on both univariate and multivariate suitability indices were consistently low and in most cases non-significant. The only significant correlation between WUA developed from one of the combined suitability indices and fish abundance was between multivariate WUA and logperch abundance at South Fork sites sampled in 1992 and 1993 ($P = 0.009$, Figure 2.12). WUA estimated using both the univariate and multivariate suitability indices from the South Fork habitat data was also significantly correlated with logperch abundance at all 28 sites ($P = 0.024$ and $P = 0.023$, respectively) and with logperch abundance at the 12 South Fork sites ($P = 0.003$ for both univariate

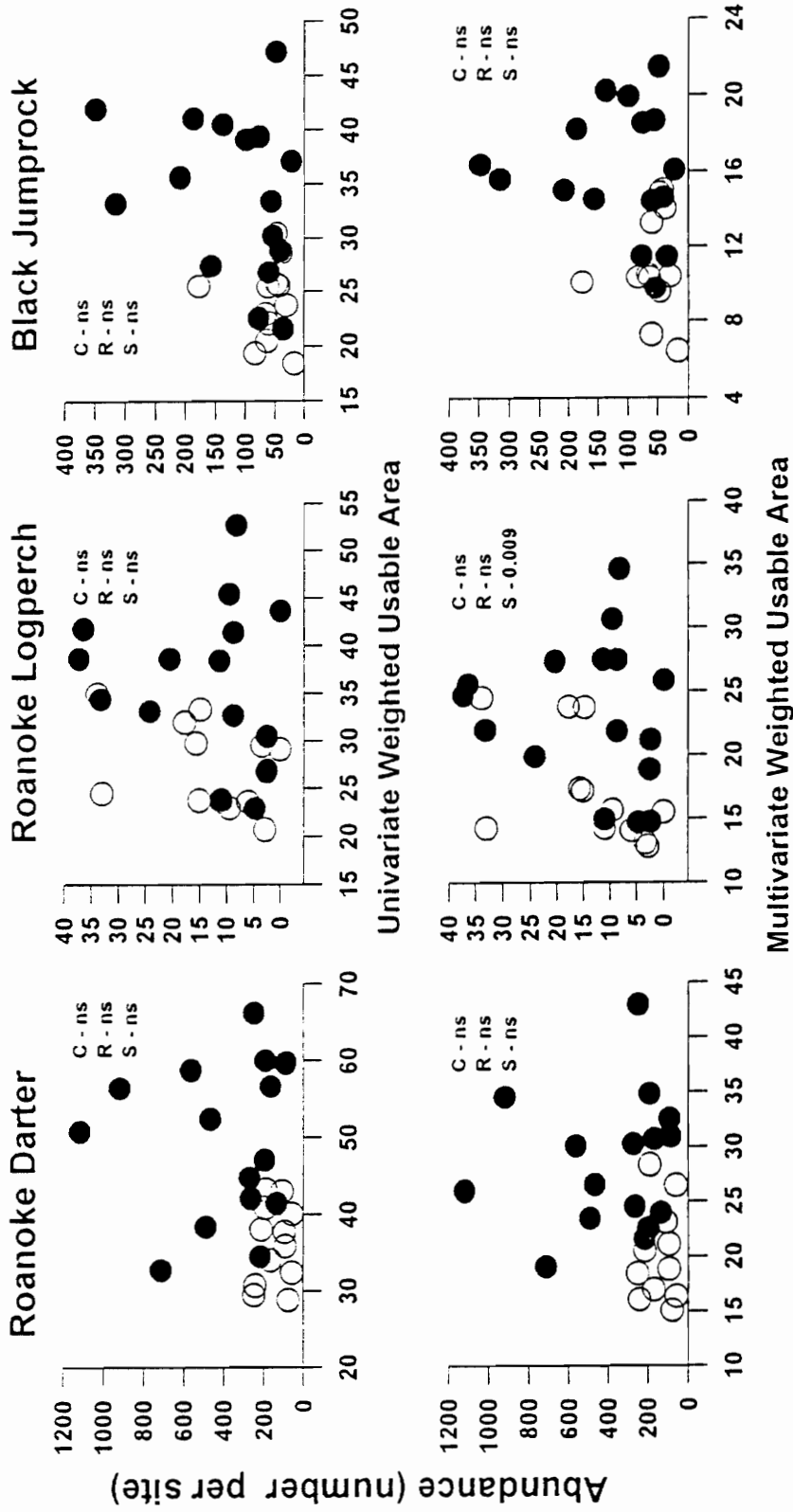


Figure 2.12. Scatterplots of weighted usable area (WUA) calculated using both the univariate and multivariate suitability indices from the combined habitat use data set and abundance of Roanoke darter, Roanoke logperch, and black jumper at 28 sites sampled on the Roanoke and South Fork Roanoke Rivers in 1991, 1992, and 1993. Open circles represent the 12 South Fork River samples, closed circles represent the 16 Roanoke River samples. P-values are given for significant correlations (Spearman's correlation coefficient, $P < 0.05$) between WUA and abundance from the 28 sites combined (C), the 16 Roanoke sites (R), and the 12 South Fork sites (S).

and multivariate WUA). Also, black jumprock abundance from all 28 sites was weakly correlated with WUA estimated using the Roanoke River univariate suitability indices ($P = 0.049$), while the correlation between the South Fork multivariate WUA estimates and jumprock abundance at the 16 Roanoke River sites approached significance ($P = 0.068$).

Discussion

Habitat Use

My first objective in this study was to determine if Roanoke darter, Roanoke logperch, and black jumprock use habitat in riffles and runs in proportion to its availability or alternatively, if they select certain types of habitat within riffles and runs. Differences in fish density among class intervals for the univariate habitat variables and among habitat combinations for the multivariate descriptors provide strong evidence that these three species do exhibit habitat selection. This result is consistent with numerous other studies showing differential habitat use by benthic riffle fishes (Thomas 1970, Greenberg 1988, Leonard and Orth 1988, Meffe and Sheldon 1988, Bain and Finn 1991, Kessler and Thorp 1993, Freeman and Freeman 1994).

The patterns of habitat use I observed for Roanoke darter, Roanoke logperch, and black jumprock are consistent with other studies of these species both in the Roanoke River basin and in other basins within Virginia. Vadas (1994), using a combination of seining and shocking techniques in the South Fork Roanoke and upper Roanoke River, identified deep, moderately fast riffles and runs as the habitat type most commonly used by logperch and jumprock while Roanoke darter were found most commonly in shallow, fast riffles. Matthews et al. (1982), using kick-set seining, observed highest abundances of Roanoke darter in swift, shallow areas of the South Fork. Burkhead (1983) found adult logperch most commonly over cobble

substrates in water depths ranging from 15 to 74 cm in depth at velocities ranging from 37 to 82 $\text{cm}\cdot\text{s}^{-1}$ using electroshocking in sites in South Fork and Roanoke Rivers during summer months. He also noted near total avoidance of silted substrates by adult logperch. Mean depth and mean column velocities of black jumprock in James River tributaries were 58 cm and 37 $\text{cm}\cdot\text{s}^{-1}$, respectively, based on underwater observation (Leonard and Orth 1988). Finally, distributions of depth, column velocity, and substrate type used by logperch and Roanoke darter at a Nottoway River site near the fall line in Virginia and by darter and black jumprock at a Smith River site in Virginia were consistent with those obtained in this study (W. E. Ensign, unpublished data). The general agreement between my data and other studies suggest that the general habitat use characteristics presented here are not simply the result of gear or site-specific factors but may be of adaptive significance for the three study species.

Although the general patterns of habitat use I observed are consistent with other studies of the same species, there were discernable differences in both multivariate and univariate habitat use characterizations between Roanoke and South Fork sites. As noted, the general pattern for all three species was increased use of deeper water in the South Fork. Furthermore, both Roanoke logperch and black jumprock tended to use higher velocity areas in the Roanoke than in the South Fork.

Differences in microhabitat use by stream fish both among sites within a drainage and among drainages have been noted in numerous studies (Matthews and Hill 1980, Power et al 1985, Angermeier 1987, Greenberg 1988, Bozek and Rahel 1992, Kwak et al. 1992, Groshens and Orth 1994, Freeman and Freeman 1994). Shifts in microhabitat use have been attributed to a number of factors, including differences in fish activity patterns among sampling periods (Shirvell and Dungey 1983, Kwak et al. 1992), presence of competitors in some reaches and not others (Fausch and White 1981, Moyle and Baltz 1985, Greenberg 1988), presence of

predators in some reaches and not others (Power 1985), differences in physiological tolerances among populations (Matthews and Hill 1980), differences in habitat availability among sites (Moyle and Baltz 1985, Ross et al. 1987, Bozek and Rahel 1992, Freeman and Freeman 1994), and trade-offs between foraging opportunities and predation pressure (Fraser and Cerri 1982, Angermeier 1987).

In this study, differences in habitat use among reaches due to differences in fish activity at the time of sampling were probably minimal. All sampling was undertaken during the same season and daily sampling occurred at all sites from 900 h to 1500 h. The two dominant behaviors observed were feeding and resting and, based on personal observations, the relative proportion of fish engaging in these behaviors seemed to be similar among reaches. The fish communities in the two reaches are similar (W. E. Ensign, unpublished data) so shifts associated with presence or absence of competitors or piscine predators also seems unlikely. There are no obvious barriers to gene flow among South Fork and Roanoke River populations of the three study species, so differential habitat utilization associated with differences in physicochemical tolerances also seems unlikely.

I cannot eliminate the possibility that differences in habitat availability or trade-offs between foraging opportunities and predation risk may have influenced differences in habitat selection between the two reaches and, given the differences in land use practices outlined in the introduction to the dissertation, this could be an important factor. Although sampling for this study focused on erosional units, qualitative observations of depositional areas during sampling lead me to believe that siltation in the Roanoke River is more extensive than in the South Fork. Silt has been shown to reduce populations of benthic insectivores (Berkman and Rabeni 1987) and has been implicated in declines of logperch populations in the Roanoke and North Fork River (Burkhead 1983, Burkhead and Jenkins 1991, Jenkins and Burkhead 1994, Ferguson et al. 1994). The increased importance of high velocity

areas in the Roanoke River could be a response to increased siltation, as areas with low velocity are more likely to be impacted by deposition of fine substrate particles.

It is possible that use of deeper areas in the South Fork are a response to differential predation pressure in the two reaches. Avian predators were rarely seen along the banks of the Roanoke River, presumably due to increased human disturbance, but both Belted Kingfisher (*Megaceryle alcyon*) and Green-backed Heron (*Butorides striatus*) were commonly seen along the rural banks of the South Fork. Success of avian piscivores is thought to increase with decreased water depth, and this may be reflected in the increased importance of deeper areas to the study species.

In summary, there was strong evidence that Roanoke darter, Roanoke logperch, and black jumprock use only a subset of the habitat available in the Roanoke and South Fork Roanoke Rivers. Although the general pattern in habitat use is similar between the two reaches, there are differences that may be attributable to anthropogenic effects. These effects may be both direct, through the introduction of additional fine substrate particles, and indirect, through behavioral changes associated with a shift in the types of predation pressure to which the species are exposed.

Comparison of Suitability Indices

Much of the literature on the use of univariate versus multivariate suitability indices focuses on technical details of function specification (e. g. univariate histogram frequency analysis versus bivariate exponential polynomial models, (Lambert and Hanson 1989, Cheslak and Garcia 1992) and other modeling constraints associated with the Physical Habitat Simulation (PHABSIM) module of the Instream Flow Incremental Methodology. Since the purpose of this study was not to develop microhabitat models for use in PHABSIM, but to develop reasonable

microhabitat models for Roanoke darter, Roanoke logperch and black jumprock, the standards used to assess the importance of interactions among variables are much simpler. First, do the separate suitability indices provide similar rankings for the different types of habitat used by the three species? Statistically, the answer to this question is a resounding "yes" for all three species. However, there were identifiable, but statistically non-significant, differences in the rankings for all three species. To paraphrase an overworked cliché, statistical non-significance does not necessarily indicate biological non-significance. Therefore, the second standard used is how well the two indices predict fish abundance when they are used to estimate WUA. Again, there was little difference in the indices; both performed poorly as indicators of the abundance of the three species.

Based on the data presented, there is no clear evidence for selection of either technique based on comparability or performance. Selection can therefore be based on the assumptions underlying the two techniques. Both indices assume that the counts of fish in individual cells either represent true densities or serve as a reasonable index to the true densities of the three species. Both indices also assume that these densities reflect preference or avoidance by the target species. Finally, as I noted previously, the univariate technique assumes that fish respond to the measured habitat variables independently. Applying the principle of Occam's Razor, the multivariate index requires fewer assumptions and, all other factors being equal, should be used rather than the univariate index.

Microhabitat Availability/Abundance Correlations

Three patterns emerge from the correlations between WUA and fish abundance. First, there was no evidence for a straightforward relationship between WUA and fish abundance for either the Roanoke darter or the black jumprock. Although black jumprock abundance at all 28 sites was weakly correlated with WUA

estimated using the Roanoke River univariate suitability index, given the number of correlations examined, this is no more than would be expected at random. Logperch abundance was positively correlated with WUA in some instances, but the relationship between the availability of preferred microhabitat and population levels was weak. Second, positive correlations between logperch abundance and the microhabitat models were limited to instances where abundance in the 12 South Fork sites were related to WUA estimated using the combined habitat use data set, or where WUA estimated using the South Fork habitat use data set was related to abundance either in all 28 sites or only in the 12 South Fork sites. Noticeably absent from these combinations are correlations between measures of abundance from the 16 Roanoke River sites and any measure of WUA or a measure of WUA estimated using the Roanoke River habitat use data set that correlates with any measure of abundance. Third, inspection of the WUA/abundance scatterplots (Figure 2.12) indicates that the abundance of the three species at sites with low WUA is consistently low, but sites with high WUA have both low and high abundances. Although the potential factors leading to these patterns are probably interrelated, for the sake of clarity I will treat each in turn.

The lack of agreement between my estimates of site quality (WUA) and fish abundance are not the first time that a habitat model has failed as predictor of organism abundance. Although numerous reasons for habitat model failures have been advanced (O'Neil and Carey 1986, Orth 1987, Gore and Nestler 1988, Fausch et al. 1988), the most reasonable and parsimonious explanation is a failure in the model's basic assumption, in this case that the availability of late summer microhabitat is the most important factor limiting populations of Roanoke darter, Roanoke logperch, and black jumprock in the upper Roanoke River during the years that I sampled. The obvious question to be addressed is whether the pattern I observed is peculiar to these three species in the Roanoke River or if it has broader

implications for other researchers attempting to develop habitat models for stream fish.

In cases where microhabitat models incorporating depth, velocity, substrate, and sometimes cover have been successful, there is clear evidence that certain configurations of these variables facilitate a function critical to the population dynamics of the study species. For example, salmonids in streams occupy focal positions that provide an optimal trade-off between availability of drifting food resources and energy expenditure (Jenkins 1969, Fausch 1984, Hill and Grossman 1994). Management activities that increased the availability of these optimal positions in the South Platte and Rio Grande rivers in Colorado resulted in an increase in both total brown trout (*Salmo trutta*) biomass and the number of brown trout larger than 35 cm total length (Shuler and Nehring 1994). Salmonid abundance has also been shown to be strongly influenced by the quantity and quality of spawning, hatching, and fry nursery habitat (Ottaway and Clarke 1981, Neitzel and Becker 1985, Anderson and Nehring 1985, Shirvell 1990). A 13 year study of 11 Colorado streams revealed that the abundance of trout in 10 of the streams was strongly correlated with the availability of either spawning or nursery habitat (Nehring and Anderson 1993). Microhabitat models have also successfully predicted the abundance of specific life stages for some centrarchids (Sabo 1993, Barret and Maughan 1994), a group that also has a voluminous literature relating various habitat configurations to the success of specific life stages.

In contrast to the extensive knowledge of the requirements of the differing life stages of centrarchids and salmonids, our knowledge of the importance of various combinations of depth, velocity, and substrate to benthic riffle fishes is limited. Although all three of the study species spawn in riffles (Jenkins and Burkhead 1994), specific habitat requirements and the effect of variation in environmental conditions are largely unknown. The occurrence of these species in

riffles during summer months is thought to be due to a combination of two factors, increased availability of food resources in riffles relative to pools (Kuehne and Barbour 1983, Schlosser 1987) and refuge from large piscivorous fish (Powers and Matthews 1983, Schlosser 1987, Power 1987, Angermeier 1992). Although the importance of predation has been demonstrated in both correlative and manipulative studies (Power and Matthews 1983, Fraser et al. 1987, Angermeier 1992) the importance of food availability is poorly documented (Petty 1994). Furthermore, the information available is general in nature and provides little guidance in determining the combination of physical variables that are of functional significance to riffle fishes. Lacking this information, it is difficult to determine the specific importance of riffle habitat in the population dynamics of Roanoke darter, Roanoke logperch, and black jumprock.

The lack of correlation between the availability of preferred habitat and riffle fish abundance is not unique to my study. Freeman and Freeman (1995) showed that amber darter (Percina antesella) display marked habitat preference in the Conasauga River, Georgia, but the availability of preferred habitat was a poor indicator of total fish abundance at 3 sites. Likewise, there was little correspondence between mottled sculpin (Cottus bairdi) abundance and physical habitat characteristics in Coweeta Creek, North Carolina (Petty 1994). In contrast, Orth and Maughan (1982) found positive correlations between late summer WUA and standing stock of orangebelly darter (Etheostoma radiosum), central stoneroller (Campostoma anomalum), and freckled madtom (Noturus nocturnus) in Glover Creek, Oklahoma. Difference in the utility of late summer habitat availability for predicting population characteristics among these studies may be due to differences in environmental variability among the benign mesic groundwater streams of the eastern United States and the harsher perennial runoff streams of Oklahoma (Poff and Ward 1989). Late summer riffle habitat is limited in Glover Creek (Orth and Maughan 1982), potentially resulting in

decreased food availability and increased exposure to predation. In contrast, riffle habitat in upland eastern warmwater streams remains relatively abundant in late summer, and therefore these presumptive factors may not limit riffle fish populations. However, given my inability to specify the functional role of riffle habitat in the population dynamics of these species, this inference is largely speculative.

The second pattern of interest is the ability (albeit limited) of my models to predict the abundance of Roanoke logperch. Two questions to be answered in regard to this result are 1) Given the similarities in trophic, reproductive and habitat use characteristics of the three species, why can microhabitat availability predict the abundance of logperch but not Roanoke darter and black jumprock, and 2) Why does microhabitat availability predict logperch abundance in the South Fork but not in the Roanoke River?

I would argue that the answer to the first question stems from differences in the life history strategies of the three species. Of the three study species, Roanoke logperch is most strongly associated with the periodic life history strategy of Winemiller and Rose (1992). Since periodic strategists delay maturity and spread reproductive effort over multiple spawning bouts, population dynamics of these species are strongly linked to factors that promote adult growth and survival. In contrast, species with an opportunistic strategy (Roanoke darter and to a lesser degree, black jumprock) mature quickly and package reproductive effort into fewer spawning bouts. Therefore, the population dynamics of opportunistic species should be linked to habitat characteristics that foster increased larval and juvenile survivorship. Since the habitat characteristics I measured were associated with adults, it should not be surprising that the significant correlations I obtained were for the periodic, not the opportunistic, species. Although there are few other studies focusing on links between habitat requirements and life history strategies, successful

salmonid and centrarchid habitat models provide indirect support for this line of reasoning. Spawning and nursery habitat most often limits populations of freshwater lotic species in these families (Shirvell 1990, Nehring and Anderson 1993, Sabo 1993), a pattern expected for equilibrial strategists (Winemiller and Rose (1992).

The differential ability of the logperch models may be related to the differences in land use patterns between the two reaches. As I have already indicated, land use patterns in the two reaches are markedly different.

Anthropogenic impacts associated with urbanization, particularly increased siltation, have a much greater influence on the Roanoke than the South Fork. Increased siltation has a number of potential effects on fish populations, including reducing diversity of invertebrate prey, limiting interstitial flow in spawning substrate and reducing the availability of winter refuge (Chutter 1969, Nuttal and Bielby 1973, Berkman and Rabeni 1987). An argument has already been made that siltation may alter habitat use by Roanoke logperch in the Roanoke study reach, and an extension of that argument to effects on population dynamics seems reasonable.

To see the final pattern of interest, a bit of minor data manipulation beyond that already carried out is necessary. If the abundance measures and estimates of WUA for all three species are scaled from 0 to 1 by dividing by the maximum observed abundance and maximum observed WUA, all three species can be plotted on equivalent scales (Figure 2.13). The pattern that emerges is that at low WUA values, you tend to see only low abundance levels while at higher WUA values, there is a scatter of both high and low abundances. This pattern is strengthened when you consider that sites sampled in this study were all composed of predominantly erosional-type habitats. Based on habitat use information, sites composed primarily of depositional habitats should provide very low WUA values. Personal observations and other studies carried out in the same system (Matthews et al. 1982, Matthews 1990, Vadas 1994) indicate the abundance of the three species in

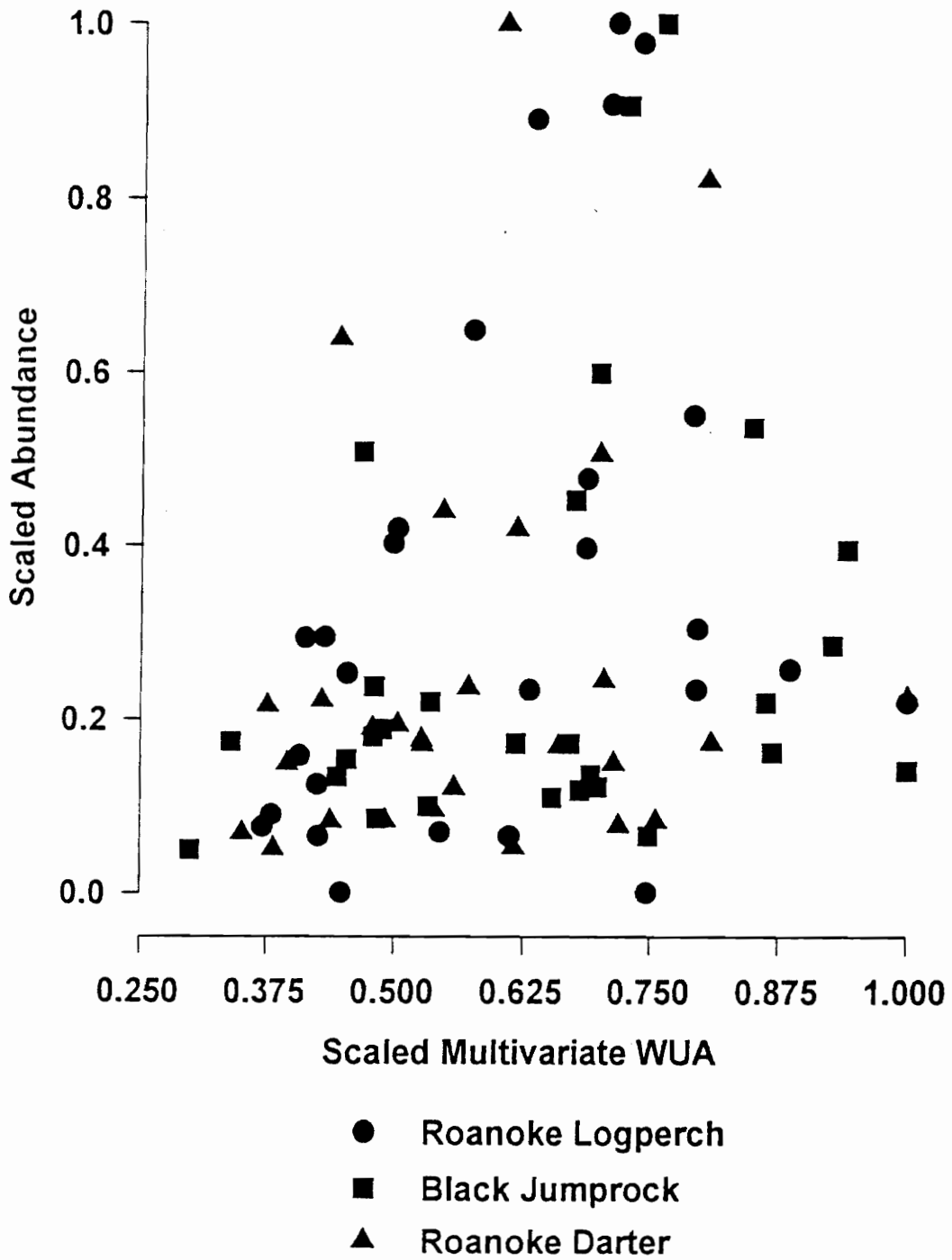


Figure 2.13. Roanoke darter, Roanoke logperch, and black jumprock scaled abundance and weighted usable area estimates from electrofishing sites sampled on the Roanoke River in 1991 and South Fork Roanoke River in 1992 and 1993.

depositional habitats during late summer is extremely low. Therefore, although points in the left tail of the WUA axis in Figure 2.13 (i.e. where scaled WUA is less than 0.25) are not available from the data presented here, other evidence supports the inference that low WUA and low abundance are strongly linked. The pattern is somewhat compromised by the absence of points in the upper right hand corner of the graph where both abundance and WUA are high. Sites with scaled WUA values greater than 0.850 are all located in the urbanized Roanoke River. Anthropogenic impacts are more severe in this reach and therefore factors other than habitat availability (e. g. water quality, exclusion of potential predators) may be limiting these populations.

In summary, although all three species showed marked evidence of differential habitat utilization, the distribution of preferred habitat was a poor predictor of fish abundance. This failure is due in part to the models' failure to link the preferred habitat types to biological functions that may or may not limit population growth and survival. My results highlight the importance of additional studies demonstrating the functional importance of various combinations of depth, substrate, and velocity for riffle fishes. For salmonids and centrarchids, much of this information is currently available and the success of microhabitat models can be demonstrated. Success of riffle fish microhabitat models will be limited until similar information is available for this group of fish. My results also indicate that microhabitat may be viewed as a necessary, but not sufficient, condition for predicting fish abundance. The possibility that other factors at other scales interact with microhabitat availability to determine riffle fish population size and distribution will be explored in the next two chapters.

CHAPTER 3

Intermediate-scale measures of habitat as predictors of benthic fish abundance in riffles

Introduction

In Chapter 2, I determined the microhabitat preference of Roanoke darter, Roanoke logperch and black jumprock by looking at habitat conditions in the cell where fish occurred. However, using conditions only in the immediate vicinity of the target organism places great emphasis on proximal spatial factors influencing habitat choice. As outlined in the introduction to the dissertation, animals may be integrating a number of different, and perhaps conflicting, environmental cues at a variety of spatial and temporal scales in the process of habitat selection. Therefore, the relatively poor predictive performance of the microhabitat models developed in the previous chapter may have resulted in part from a failure to incorporate information from larger spatial scales. Current ecological theory, as well as a number of empirical studies provide a potential conceptual framework for addressing these larger spatial scales. For example, Dunning et al. (1992) identified four ecological processes (landscape complementation, landscape supplementation, source-sink relationships, and neighborhood effects) that influence the abundance and distribution of organisms in heterogenous landscapes (i.e. in the real world). The first two of these processes seem most applicable to addressing questions of habitat selection at levels larger than the microhabitat scale but still remaining within a single riffle-run unit.

Landscape complementation is important when an organism requires differing, non-substitutable resources (Tilman 1982) at different points in time and these resources are patchily distributed across the landscape. Movement among

patches has an associated cost, therefore areas where many types of patches occur in close proximity to one another are able to support higher densities of the organism than areas where the differing patch types are widely separated (Dunning et al 1992). The importance of landscape complementation has been empirically demonstrated for woodland birds (Petit 1989), salt marsh fishes (McIvor and Odum 1988), and checkerspot butterflies (Weiss et al. 1988) and can be reasonably extended to stream fish (Schlosser 1991). For example, areas with high food abundance may provide excellent foraging opportunities, but if these areas also contain potential predators then habitat providing refuge also may be required (Werner et al. 1983, McIvor and Odum 1988).

Landscape supplementation occurs when a patch of a needed resource occurs in close proximity to other patches of either the same resource or a similar, substitutable resource (Dunning et al. 1991). A habitat patch may be too small to support the proximal needs of an organism, but a cluster of similar-sized patches with equivalent resources may be sufficient. Population effects of landscape supplementation have been demonstrated for hazel grouse (Swenson 1993), grassland rodents and snakes (Robinson et al. 1992), and bank voles (Vanapeldoorn et al. 1992) and again, can be reasonably extended to stream fish (Schlosser 1991).

In the previous chapter, I assumed that fish select a cell independently of the types of habitat available in adjacent cells. Not surprisingly, there was noticeable variation in fish densities in both suitable and unsuitable cells. Not all cells with high suitability values contained the target species and the target species was present in some cells receiving low suitability values. However, two cells with the same combination of depth, velocity, substrate, and siltation received the same suitability value, despite the possibility that the first cell may have been surrounded by poor habitat and the second by good or excellent habitat. If the assumption that fish select a cell independently of surrounding habitat characteristics is valid (i. e. no

supplementation or complementation occurs), then habitat characteristics around the target cell should have little utility in explaining the variability in fish densities among target cells with similar suitability values. Conversely, if cells do not function independently and either complementation or supplementation occurs, cell suitability incorporating measures of habitat conditions in both adjacent and target cells should explain a greater portion of the variability in fish density than suitabilities incorporating only target cell suitabilities. Therefore, the null hypothesis I tested was that for a given suitability level, target fish densities did not differ as a function of habitat conditions in adjacent cells. The alternative hypothesis was that adjacent cell conditions explained a significant portion of the variability in target cell fish densities for a given suitability level.

The second approach I used in this study focused on potential supplementation effects in a single riffle/run unit. To develop a testable hypothesis, I assumed that each cell represented an individual habitat patch. I also assumed that movement from one patch of suitable habitat to another patch of suitable habitat within a given riffle had an associated cost (temporary cessation of foraging or perhaps exposure to increased predation risk). Given these assumptions, the concept of supplementation suggests that riffles with highly aggregated suitable habitat should support higher fish abundance than riffles where a similar total area of suitable habitat is fragmented into smaller or widely separated patches. The null hypothesis was that, given similar total areas of suitable habitat, there should be no difference in fish abundance at sites where habitat is contiguous and sites where habitat is fragmented. The alternative was that riffles with highly aggregated habitat should support higher abundances than riffles where habitat is fragmented.

Given this framework and the two stated null hypotheses, I had four objectives in this study: 1) develop descriptors of habitat conditions in cells adjacent to target cells with similar suitability values, 2) determine the utility of these

descriptors in explaining variability in density of the three target species, 3) determine the importance of spatial contiguity of suitable habitat within riffles in determining the abundance of the three target species, and 4) determine if incorporation of intermediate scale measures of habitat suitability into the microhabitat models developed in the previous chapter resulted in increased ability to predict abundance of Roanoke darter, Roanoke logperch, and black jumprock.

Methods

Field Data Collections

Characteristics of the three study species, Roanoke darter, Roanoke logperch, and black jumprock, have already been given in the introduction to the dissertation. Data collection methods, site characteristics, and abundance estimation techniques for this chapter are the same as for Chapter 2 and have been fully described in the Methods section for that chapter.

Importance of Adjacent Cell Habitat

The approach in this chapter is explicitly cell based. As in the last chapter, a cell is considered to be a rectangular area (3 m wide by 15 m long) centered on the point where habitat measurements were taken during the course of field sampling. For this analysis, adjacent habitat cells are those sharing either a side or a corner with the target cell (queen's case definition of a join, Upton and Fingleton 1985). By using the queen's case, the full range of variation in measured variables surrounding the target cell is taken into consideration. Depending on its location in the site, each target cell has from three to eight adjacent cells. For each of the target cells, 10 separate habitat variables were developed based on observed values of depth, water column velocity, substrate, and siltation in adjacent cells. The variables were mean depth, mean column velocity, maximum depth, maximum column velocity, minimum depth, minimum column velocity, depth coefficient of variation, column velocity coefficient of variation, proportion of adjacent cells with coarse substrate,

and the proportion of adjacent cells with siltation ratings less than 4 (a measure of siltation).

The importance of adjacent cell habitat may vary as a function of habitat available in the target cell, therefore it seems reasonable to stratify the target cells by a measure of target cell suitability. For each of the three study species, the population of target cells were divided into 4 equal-sized classes by assigning a suitability rating based on the multivariate suitability index developed in the previous chapter. Cells in the lowest quartile of suitability values were given a rating of poor, cells in the second lowest quartile were assigned a fair rating, cells in the second highest quartile were rated good, and cells in the highest quartile were rated excellent. In order to reduce the number of adjacent cell variables considered and minimize correlations among variables, a separate principal components analysis was carried out on the adjacent cell variables for target cells in each of the four suitability classes. Only those components with eigenvalues greater than 1 (i. e. components that explained a greater proportion of the variation in the data set than a single variable) were retained for the next step in the analysis.

For each of the retained components, I classified each cell as having either a high (component score greater than or equal to the median score) or low (component score less than the median score) value for that component. Individual adjacent cell classes were developed for each possible combination of high or low scores across all retained components, giving a total of 2^n possible classes for a given suitability rating, where n equals the number of retained components. To determine if adjacent cell habitat explained variability in fish density within a given suitability rating, I carried out a Kruskal-Wallis test on the component score combination classes.

Combined Microhabitat-Adjacent Cell Suitability Site Ratings

For species where the results of the Kruskal-Wallis tests indicated that adjacent cell suitability had a significant effect on target cell densities for any of the

four suitability classes, I used both the multivariate suitability index developed in the previous chapter and the results obtained from the Kruskal-Wallis test to develop site quality ratings for each of the 28 electroshocking sites sampled on the Roanoke and South Fork Roanoke in 1991, 1992, and 1993. At each site, cells with a multivariate suitability index value falling within a suitability class (i.e., poor, fair, good, or excellent) that showed no significant effect of adjacent cell conditions were assigned the mean fish density for that class of the multivariate suitability index. For cells in a suitability class where adjacent cell conditions had a significant effect, cells were jointly classified on the basis of their multivariate suitability index value and their adjacent cell principal component class and assigned a mean fish density based on that joint classification. For each site the estimated cell densities were summed and the total used as the habitat quality rating for that site. Spearman's correlation coefficient was used to determine agreement between site ratings and observed abundance.

Spatial Distribution of Suitable Habitat

The data for this analysis were drawn from the 28 sites where electroshocking estimates were obtained. Habitat data at these sites were spatially referenced in the same manner as at the snorkeling sites described in Chapter 2. A problem that arises when habitat relationships are examined within a patch suitability framework is how to define suitable and unsuitable patches of habitat. Since there is no way to determine a priori what fish truly prefer, I have chosen to use different levels of the multivariate suitability index which result in a predetermined proportion of the cells at all 28 sites being designated as suitable. For each species, four different levels of suitability were used that resulted in approximately 5% of the cells being considered suitable, approximately 10% of the cells being suitable, approximately 25% of the cells being suitable, and approximately 50% of the cells

being designated suitable.

For each suitability level, individual cells were coded as either 1 (= suitable) or 0 (= unsuitable). The resulting data sets were entered into ARC-INFO and spatially explicit grid and polygon coverages developed for each site. To simplify the analysis, it was assumed that each of the measured habitat points occurred at the center of a square with sides of unit length. For each of the separate suitability levels for each of the species, ARC-INFO was used to generate two measures of the abundance and spatial arrangement of suitable habitat at each of the 28 sites.

First, the total number of cells coded 1 (suitable) was determined and this value was used as a measure of the total area of suitable habitat available at each site. Second, the number of joins (two cells sharing a common side) between cells with suitable habitat was determined. I considered cells "joined", if they shared at least one side (rook's case definition of a join, Upton and Fingleton 1985). I chose to eliminate cells sharing only a single corner (bishop's case definition of a join) since the concept underlying landscape supplementation is that suitable patches in close proximity provide better habitat due to reductions in the cost of movement among patches. An alternative way of stating the underlying mechanism is that supplementation increases the probability of movement between patches. The probability of movement across a bishop's case join is obviously less than the probability of movement across the rook's case join and in the interest of simplifying the analysis, I considered bishop's case joins to be equivalent to unconnected cells. Since the number of possible joins is dependent on the total number of suitable cells at a site, the number of joins observed at a site was divided by the maximum number of joins possible given the number of suitable cells to generate a join count ratio. A join count ratio approaching one indicates that suitable habitat at a site is highly contiguous with many shared sides between cells. A join count ratio

approaching 0 indicates suitable habitat at the site is highly fragmented, with many individual patches separated by areas of unsuitable habitat.

Ideally, an experimental test of the null hypothesis stated in the introduction would involve creating multiple sites with equal areas of suitable habitat and differing degrees of contiguity, allowing fish to colonize and reach equilibrium densities, and then use classical experiment station ANOVA to test for differences among the differing contiguity levels. Unfortunately, real streams are neither ideal nor classical, as both the area of suitable habitat and the join count ratio vary continuously among sites. Therefore the approach I used was to look at univariate correlations (Spearman's correlation coefficient) between abundance of the three target species and the two spatial variables for each of the four suitability levels. These relationships are likely to vary as a function of stream size, so in addition to carrying out this analysis for the combined data set, I also looked at correlations among the variables for reduced data sets from Roanoke River sites and South Fork Roanoke sites. In addition, I carried out a multiple regression analysis with area of suitable habitat and join count ratio as independent variables and fish abundance as the dependent variable. Separate regression equations were developed for all three species, all four suitability levels, and all three data sets (combined, Roanoke, and South Fork).

Composite Model

In order to determine if the intermediate scale measures of habitat suitability developed in the previous two sections provide additional predictive capabilities, variables shown to be correlated with darter, logperch, and jumprock abundance were used as independent variables along with the multivariate WUA estimate developed in Chapter 2 in a multiple regression analysis with fish abundance from the 28 electroshocking sites as the dependent variable. Backward variable selection was used to eliminate non-significant variables (partial F-test, $P > 0.15$).

Results

Importance of Adjacent Cell Habitat

Principal components analysis (PCA) on adjacent cell variables retained 3 components for all four suitability classes for Roanoke darter (Table 3.1), Roanoke logperch (Table 3.2), and black jumprock (Table 3.3). Variance explained by the retained components ranged from 71% for the black jumprock good suitability class (Table 3.3) to 78% for the Roanoke logperch poor suitability class (Table 3.2).

With a few exceptions, variable loadings on the first two components were consistent across both species and suitability levels. The first component (PC I) loaded heavily on velocity variables. Exceptions to this pattern were high loadings on depth coefficient of variation (CV) for the Roanoke darter fair suitability class (Table 3.1) and minimum depth for the logperch good suitability class (Table 3.2). Siltation also received high loadings for the poor suitability class for all three species (Tables 3.1, 3.2, and 3.3) and for the logperch excellent suitability class (Table 3.2). The second component (PC II) loaded most heavily on depth variables (Tables 3.1, 3.2, and 3.3) with the exception of the Roanoke darter good suitability class where PC II loaded heavily on mean and maximum velocity and coarse substrate (Table 3.1). Variables associated with PC III were not as consistent as for the first two components, but generally loaded heavily on maximum depth and maximum velocity (Tables 3.1, 3.2, and 3.3). Mean velocity also loaded on PC III for the Roanoke darter and black jumprock poor suitability classes (Tables 3.1 and 3.3, respectively), for the Roanoke logperch and black jumprock good suitability classes (Tables 3.2 and 3.3, respectively), and for the darter and logperch excellent suitability classes (Tables 3.1 and 3.2, respectively).

Kruskal-Wallis tests of Roanoke darter, Roanoke logperch, and black jumprock cell densities showed significant differences ($P < 0.05$) among the 8 PCA classes for at least one of the four suitability classes for all three species. Roanoke

Table 3.1. Variable loadings, eigenvalues, and proportion of variance explained for the three components retained by the principal components analysis of adjacent cell habitat characteristics for Roanoke darter. Separate analyses were conducted for target cells classified as poor, fair, good or excellent habitat based on multivariate suitability values developed in Chapter 2. Table entries are variable loadings and dashes indicate loadings between 0.399 and -0.399. The number of target cells used in each analysis are given in parentheses.

Variable	Poor Suitability (n = 120)			Fair Suitability (n=111)			Good Suitability (n=82)			Excellent Suitability (n=217)		
	PC I	PC II	PC III	PC I	PC II	PC III	PC I	PC II	PC III	PC I	PC II	PC III
Mean Depth	-	0.474	-	-	0.557	-	-	-	0.432	-	0.609	-
Maximum Depth	-	-	0.466	-	0.500	-	-	-	0.600	-	0.612	-
Minimum Depth	-	0.576	-	-	0.445	-	0.422	-	-	-	-	-
Depth CV	-	-0.415	-	-0.401	-	-	-	-	-	-	-	-
Mean Velocity	-0.443	-	-	-	-	0.446	-	0.501	-	-	-	0.526
Maximum Velocity	-	-	0.503	-	-	0.640	-	0.458	0.422	-	-	0.711
Minimum Velocity	-	-	-	0.481	-	-	0.438	-	-	0.444	-	-
Velocity CV	-	-	-	-0.475	-	-	-0.441	-	-	-0.440	-	-
Coarse Substrate	-	-	-	-	-	-	-	0.405	-	-	-	-
Siltation	0.439	-	-	-	-	-	-	-	-	-	-	-
Proportion of Variance	37.5	26.1	14.0	29.6	26.7	16.5	35.0	22.8	17.0	34.0	21.0	16.9

Table 3.2. Variable loadings, eigenvalues, and proportion of variance explained for the three components retained by the principal components analysis of adjacent cell habitat characteristics for Roanoke logperch. Separate analyses were conducted for target cells classified as poor, fair, good or excellent habitat based on multivariate suitability values developed in Chapter 2. Table entries are variable loadings and dashes indicate loadings between 0.399 and -0.399. The number of target cells used in each analysis are given in parentheses.

Variable	Poor Suitability (n = 124)			Fair Suitability (n=125)			Good Suitability (n=145)			Excellent Suitability (n = 136)		
	PC I	PC II	PC III	PC I	PC II	PC III	PC I	PC II	PC III	PC I	PC II	PC III
Mean Depth	-	-	-	-	0.484	-	-	0.557	-	-	0.514	-
Maximum Depth	-	-	-	-	-	0.624	-	0.655	-	-	-	0.427
Minimum Depth	-	0.560	-	-	-	-	0.409	-	-	-	0.569	-
Depth CV	-	-0.450	-	-	-	-	-	-	-	-	-0.406	-
Mean Velocity	-0.429	-	-	-	-	-	-	-	0.464	-	-	0.448
Maximum Velocity	-	-	-	-	-0.422	0.469	-	-	0.724	-	-	0.680
Minimum Velocity	-	-	-	0.429	-	-	-	-	-	-0.444	-	-
Velocity CV	-	-	-	-0.434	-	-	-	-	-	0.436	-	-
Coarse Substrate	-	-	0.678	-	-	-	-	-	-	-	-	-
Siltation	0.425	-	-	-	-	-	-	-	-	0.416	-	-
Proportion of Variance	41.7	23.7	13.0	37.1	20.2	18.0	37.9	19.2	15.1	32.0	26.8	15.2

Table 3.3. Variable loadings, eigenvalues, and proportion of variance explained for the three components retained by the principal components analysis of adjacent cell habitat characteristics for black jumprock. Separate analyses were conducted for target cells classified as poor, fair, good or excellent habitat based on multivariate suitability values developed in Chapter 2. Table entries are variable loadings and dashes indicate loadings between 0.399 and -0.399. The number of target cells used in each analysis are given in parentheses.

Variable	Poor Suitability (n = 116)			Fair Suitability (n=117)			Good Suitability (n=122)			Excellent Suitability (n=122)		
	PC I	PC II	PC III	PC I	PC II	PC III	PC I	PC II	PC III	PC I	PC II	PC III
Mean Depth	-	0.476	-	-	-	-	-	0.630	-	-	0.595	-
Maximum Depth	-	-	0.541	-	-	0.405	-	0.609	-	-	0.501	0.409
Minimum Depth	-	0.582	-	-	0.519	-	-	-	-	-	0.502	-
Depth CV	-	-	-	-	-0.484	-	-	-	-	-	-	-
Mean Velocity	-0.468	-	-	-0.435	-	0.401	-	-	0.474	0.425	-	-
Maximum Velocity	-	-	0.411	-	-	0.659	-	-	0.739	-	-	0.635
Minimum Velocity	-	-	-	-	-	-	0.457	-	-	0.414	-	-
Velocity CV	-	-	-	-	-	-	-0.419	-	-	0.443	-	-
Coarse Substrate	-	-	0.411	-	-	-	-	-	-	-	-	-
Siltation	0.426	-	-	0.444	-	-	-	-	-	-	-	-
Proportion of Variance	34.2	26.0	15.7	35.0	27.5	13.9	35.3	20.1	15.7	33.6	24.8	14.6

Roanoke darter densities differed among PCA classes for the fair suitability class ($P = 0.018$, Figure 3.1), logperch densities differed among PCA classes for poor ($P = 0.035$, Figure 3.2), fair ($P = 0.013$, Figure 3.2), and good ($P = 0.004$, Figure 3.2) suitability classes, while black jumprock densities differed among PCA classes for the good suitability class ($P = 0.034$, Figure 3.3).

In the fair suitability class, Roanoke darter densities were highest in cells adjacent to shallow, fast areas and lowest in cells adjacent to deep, fast areas (Table 3.1, Figure 3.1). Logperch densities in cells in the poor, fair, and good suitability classes were higher in areas adjacent to deep, fast areas, while densities in fair and good suitability cells were lower if adjacent to slow, shallow areas (Table 3.2, Figure 3.2). Black jumprock densities in good suitability cells were highest when adjacent to areas with uniformly moderate to high velocity water and lowest in cells adjacent to areas with at least some low velocity water (Table 3.3, Figure 3.3).

Combined Microhabitat-Adjacent Cell Suitability Site Ratings

Since there were significant differences for at least one of the suitability classes for all three species, a site quality rating combining the multivariate suitability indices developed in the previous chapter and the PCA classes was calculated for each of the 28 sites where electroshocking abundance estimates were obtained. Correlations between the combined site quality rating and observed abundance were not significant for any of the three species ($P > 0.05$, Spearman's correlation coefficient), although the correlation between logperch abundance and site quality approached significance ($P = 0.063$).

Spatial Distribution of Suitable Habitat

There were no significant univariate correlations (Spearman's correlation coefficient, $P > 0.05$, Figure 3.4) between Roanoke darter abundance and either area of suitable habitat (AREA) or the join count ratio (JNCT) for any of the four suitability levels (5%, 10%, 25% or 50%), across the three data sets (combined,

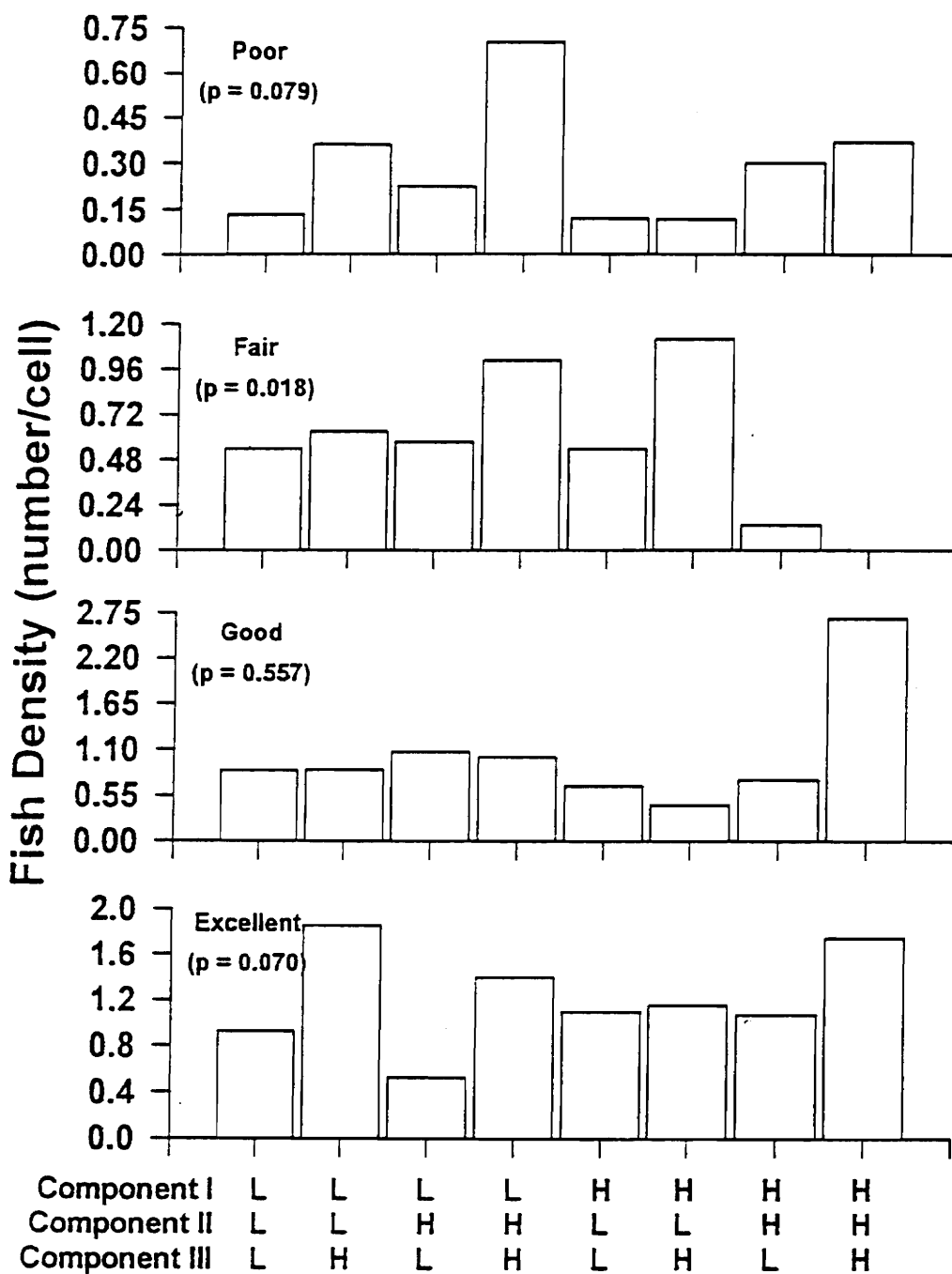


Figure 3.1. Mean Roanoke darter densities (# of fish per cell) in target cells as a function of target cell suitability class and principal component score class. Scores from PCA are either high (H = greater than or equal to median score) or low (L = less than median score). The numbers in parentheses are the significance level of the Kruskal-Wallis test for overall differences in median densities among classes within a given suitability level.

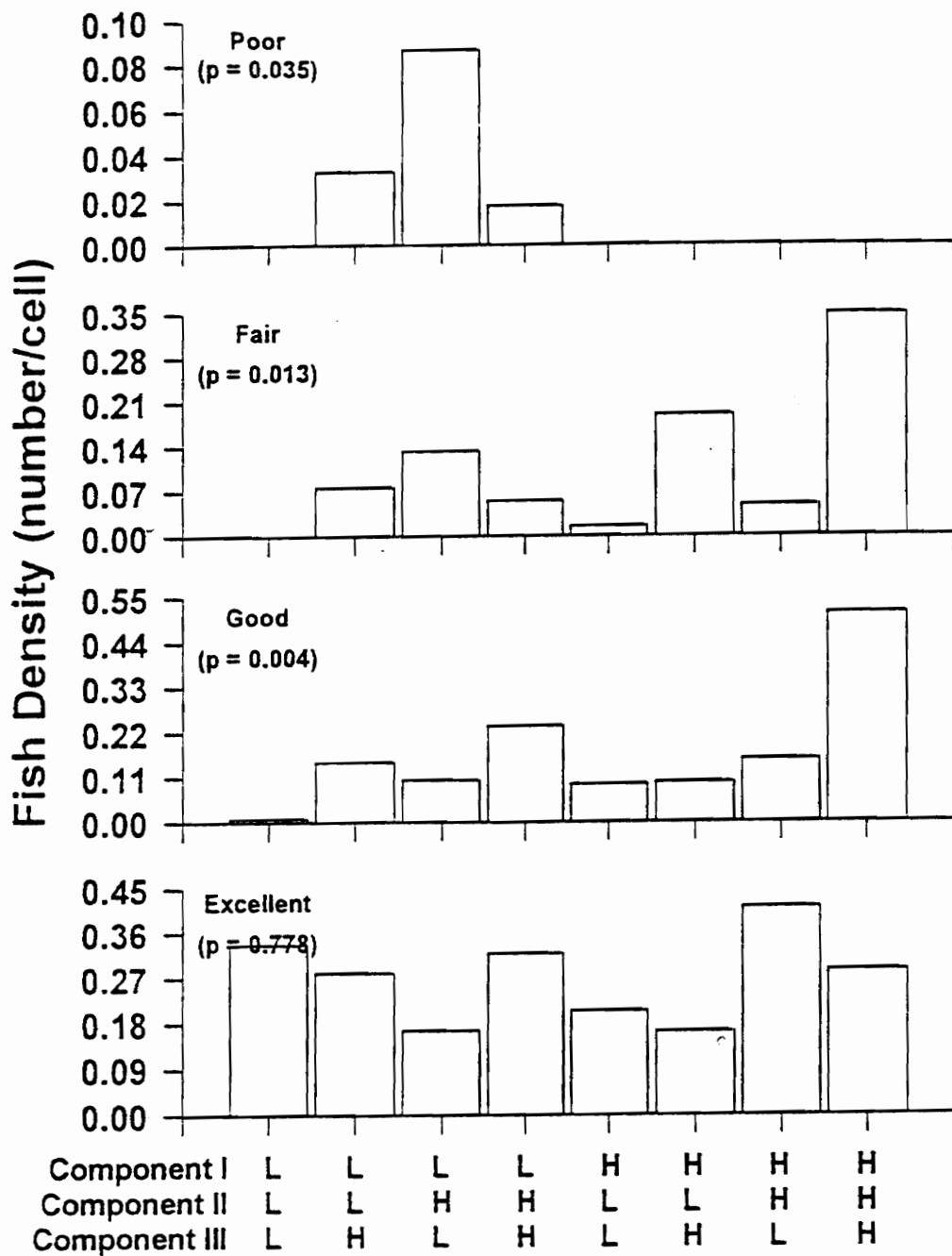


Figure 3.2. Mean Roanoke logperch densities (# of fish per cell) in target cells as a function of target cell suitability class and principal component score class. Scores from PCA are either high (H = greater than or equal to median score) or low (L = less than median score). The numbers in parentheses are the significance level of the Kruskal-Wallis test for overall differences in median densities among classes within a given suitability level.

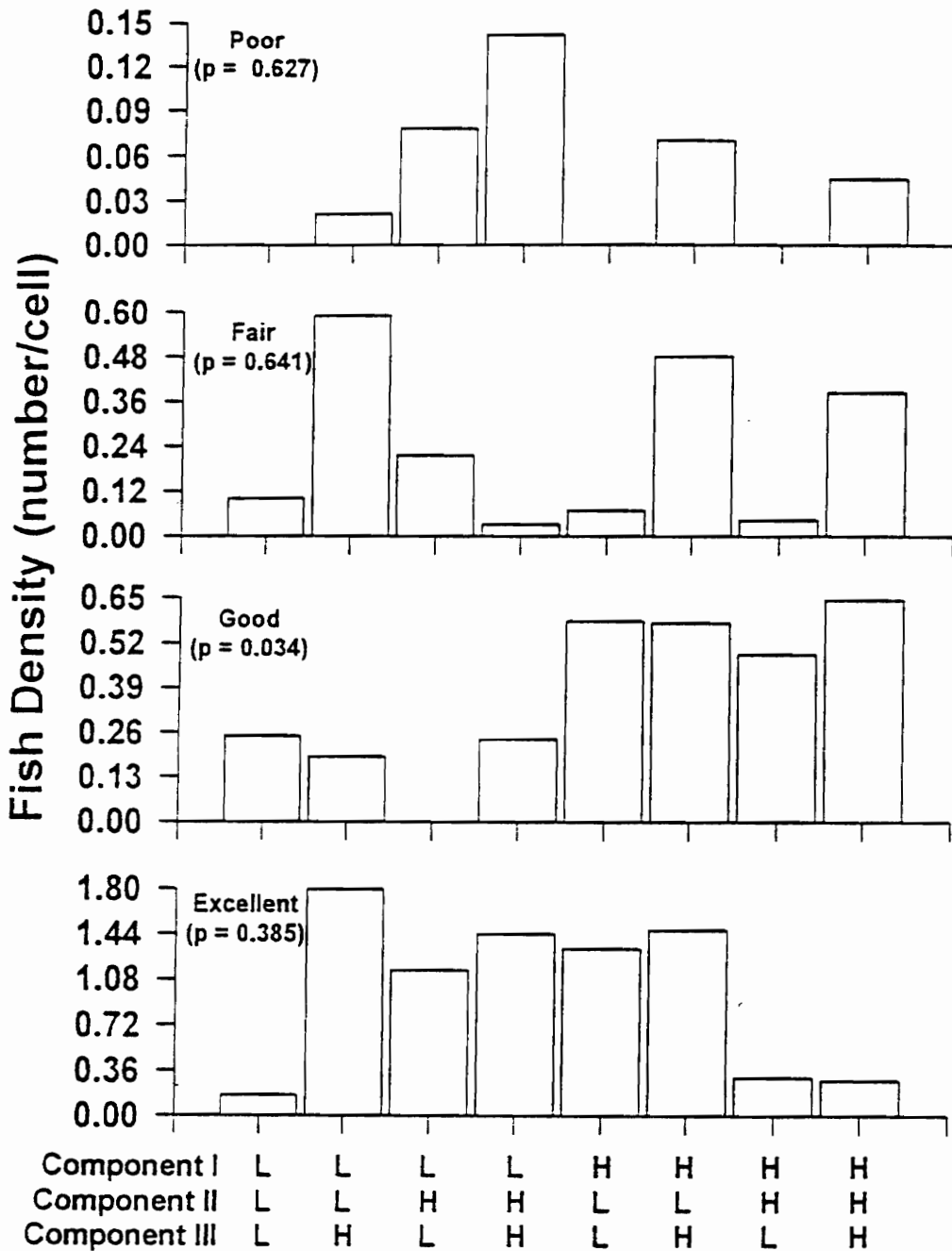


Figure 3.3. Mean black jumprock densities (# of fish per cell) in target cells as a function of target cell suitability class and principal component score class. Scores from PCA are either high (H = greater than or equal to median score) or low (L = less than median score). The numbers in parentheses are the significance level of the Kruskal-Wallis test for overall differences in median densities among classes within a given suitability level.

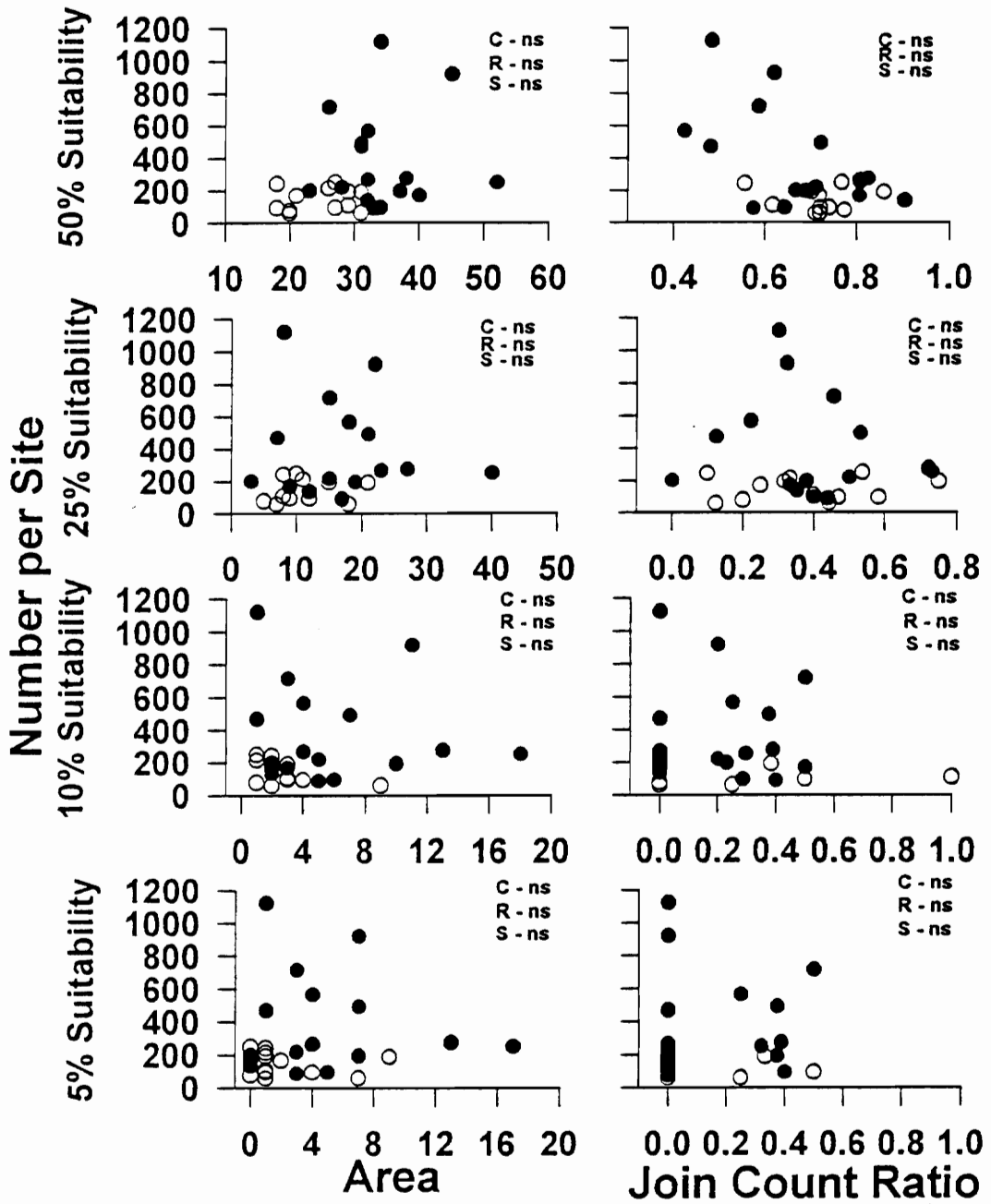


Figure 3.4. Scatterplots of Roanoke darter abundance (# of fish per site) versus area of suitable habitat (# of cells per site) and the join count ratio for the four levels of cell suitability defined in the text. Closed circles are from 16 Roanoke River sites sampled in 1991, open circles are from the 12 South Fork Roanoke sites sampled in 1992 and 1993. P-values for significant univariate correlations (Pearson's correlation coefficient, $P < 0.05$) between abundance and both area and join count ratio are given on each graph for the combined data set (C), the Roanoke data set (R) and the South Fork data set (S).

Roanoke, and South Fork). Roanoke logperch abundance was positively correlated with AREA for the combined data set at both the 10% and 5% suitability levels ($P = 0.016$ and $P < 0.001$, respectively), for the Roanoke River data set at the 5% suitability level ($P = 0.002$) and for the South Fork data set at the 10% level ($P = 0.009$, Figure 3.5). Abundance of logperch was positively correlated with JNCT at the 5% level for the combined data set ($P = 0.004$) and the Roanoke data set ($P = 0.013$), but negatively correlated with JNCT for the South Fork data set at the 10% level ($P = 0.002$, Figure 3.5). Black jumprock abundance was negatively correlated with JNCT for all three data sets at the 50% suitability level (combined, $P = 0.005$; Roanoke, $P = 0.034$, South Fork, $P = 0.041$; Figure 3.6) and positively correlated with AREA for the Roanoke data set ($P = 0.012$, Figure 3.6).

Significant multiple regression models (F-test, $P < 0.05$) relating abundance jointly to AREA and JNCT were obtained for all three species from at least one of the data set/suitability combinations (Table 3.4). For the combined data set, the Roanoke darter model at the 50% suitability level, the Roanoke logperch model at the 5% suitability level, and the black jumprock model at the 50% suitability level all explained a significant portion of abundance variation ($R^2 = 0.423$, $P = 0.001$; $R^2 = 0.337$, $P = 0.006$; $R^2 = .327$, $P = 0.007$ for darter, logperch and jumprock respectively, Table 3.4). Both AREA and JNCT contributed significantly to the models for Roanoke darter and black jumprock (partial t-test $P < 0.05$), but AREA was the only significant term in the logperch model. For the Roanoke data set, 47% of the variation in Roanoke logperch abundance was explained by the multiple regression model, while 39% of the variation in jumprock abundance was explained by the 10% suitability model. For both of these models, AREA was the only significant term. Finally, 61% of the variation in jumprock abundance was explained by the 10% suitability model for the South Fork data set and both terms were significant.

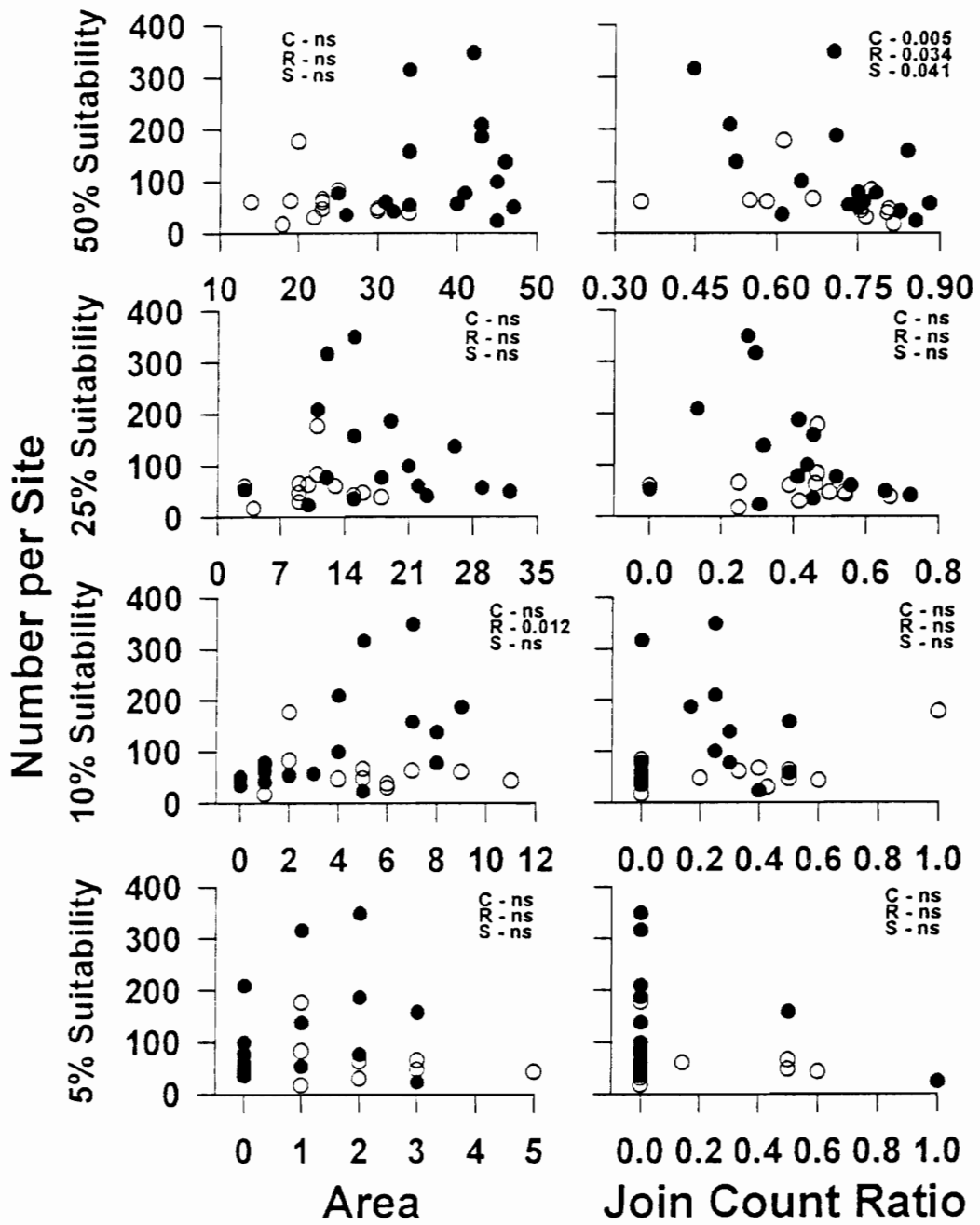


Figure 3.6. Scatterplots of black jumprock abundance (# of fish per site) versus area of suitable habitat (# of cells per site) and the join count ratio for the four levels of cell suitability defined in the text. Closed circles are from 16 Roanoke River sites sampled in 1991, open circles are from the 12 South Fork Roanoke sites sampled in 1992 and 1993. P-values for significant univariate correlations (Pearson's correlation coefficient, $P < 0.05$) between abundance and both area and join count ratio are given on each graph for the combined data set (C), the Roanoke data set (R) and the South Fork data set (S).

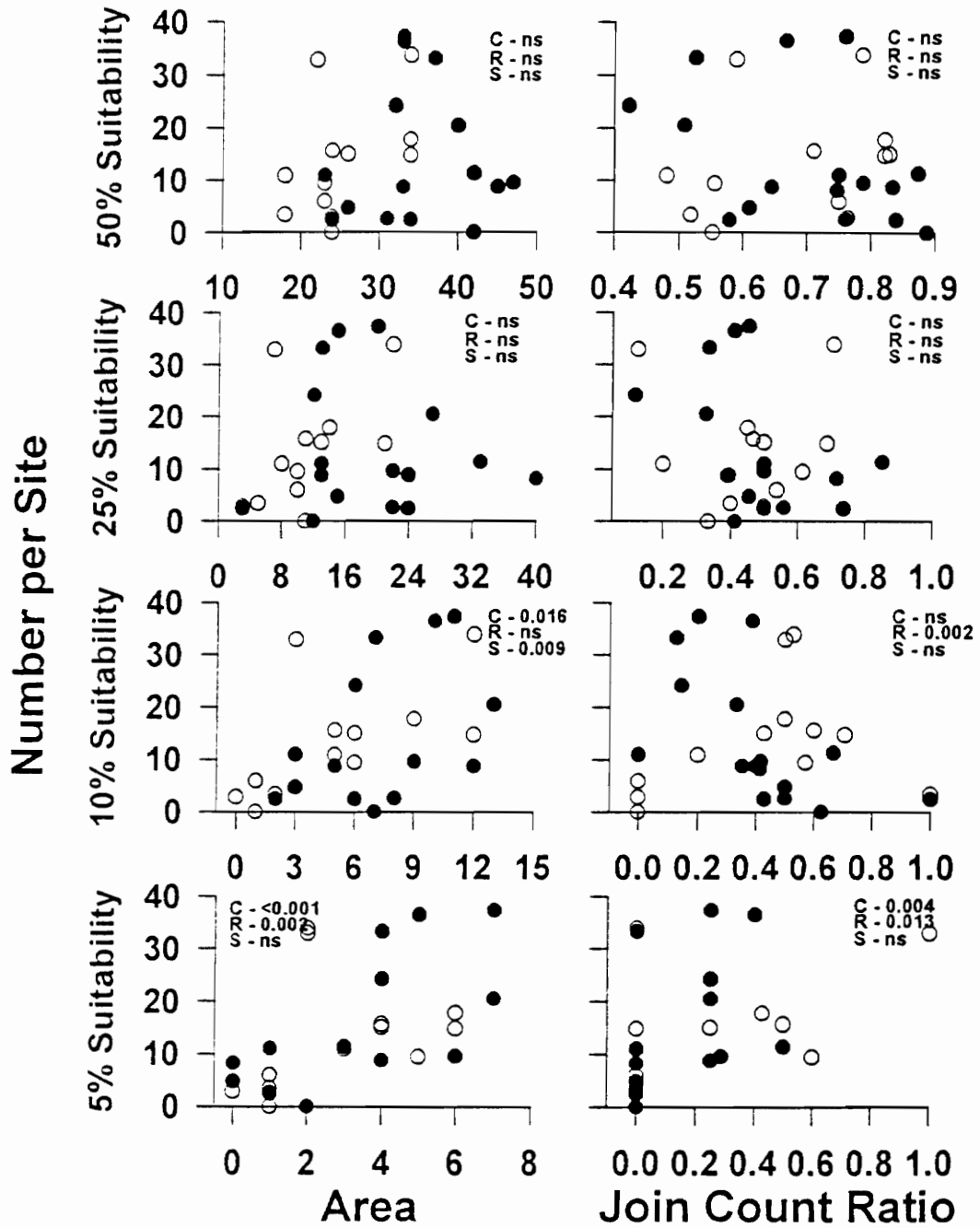


Figure 3.5. Scatterplots of Roanoke logperch abundance (# of fish per site) versus area of suitable habitat (# of cells per site) and the join count ratio for the four levels of cell suitability defined in the text. Closed circles are from 16 Roanoke River sites sampled in 1991, open circles are from the 12 South Fork Roanoke sites sampled in 1992 and 1993. P-values for significant univariate correlations (Pearson's correlation coefficient, $P < 0.05$) between abundance and both area and join count ratio are given on each graph for the combined data set (C), the Roanoke data set (R) and the South Fork data set (S).

Table 3.4. Significant multiple regression models relating area of suitable habitat (ARE) and the join count ratio (JNCT) to Roanoke darter, Roanoke logperch, and black jumprock abundance from all 28 sites sampled in 1991, 1992, and 1993 (Combined data set), the 16 Roanoke River sites sampled in 1991 (Roanoke data set), or the 12 South Fork Roanoke sites sampled in 1992 and 1993 (South Fork data set). Suitability level indicates the proportion of cells designated as suitable habitat. Coefficient P-values are based on partial t-tests and the model P-values are based on the overall F-test. R² is the coefficient of multiple determination. Scatterplots displaying the raw data are presented in Figures 3.7 (Roanoke darter), 3.8 (Roanoke logperch) and 3.9 (black jumprock).

Data Set	Suitability Level	Model	P-value		R ²
			Coefficient	Model	
Roanoke Darter					
Combined	50%	Abundance = 787.287 + 12.604·ARE - 1281.503·JNCT	0.021 0.001	0.001	0.423
Roanoke Logperch					
Combined	5%	Abundance = 4.682 + 2.270·ARE + 11.353·JNCT	0.026 0.183	0.006	0.337
Roanoke	5%	Abundance = 2.480 + 3.801·ARE - 3.304·JNCT	0.023 0.874	0.016	0.469
Black Jumprock					
Combined	50%	Abundance = -192.563 + 3.635·ARE - 304.669·JNCT	0.018 0.009	0.007	0.327
Roanoke	10%	Abundance = 55.287 + 25.181·ARE - 203.385·JNCT	0.014 0.185	0.041	0.388
South Fork	10%	Abundance = 59.808 - 6.492·ARE + 100.491·JNCT	0.047 0.007	0.015	0.608

Scatterplots jointly displaying fish abundance, JNCT, and AREA provide additional information for assessment of the adequacy of the multiple regression models. The Roanoke darter model from the combined data set at the 50% suitability level has no obvious outliers that could unduly influence the results of the regression and the joint distribution of JNCT and AREA display little evidence of collinearity between the two independent variables (Figure 3.7). The importance of AREA and the lack of a significant JNCT effect are confirmed for the Roanoke logperch models (Figure 3.8). The difference in significance and the contrasting signs of the JNCT coefficient are most probably due to a single outlier displaying low AREA and high JNCT values in the logperch combined data set. The black jumprock scatterplots for the combined 50% suitability data set and the Roanoke 10% suitability data set are similar to the Roanoke darter scatterplot, with no obvious outliers and little evidence of collinearity between the independent variables (Figure 3.9). In contrast, the joint distribution of AREA and JNCT for the jumprock 10% suitability data set from the South Fork displays two distinct clumps of observations with no intervening point, suggesting collinearity and artificial inflation of significance levels for both the overall model and the partial t-test of the coefficients. In summary, combining the results of the regression significance test and qualitative observations from the scatterplots indicate that the Roanoke darter model, the combined 50% model for the black jumprock, and the Roanoke 10% model for the jumprock explain a significant portion of the variation in the abundance of the two species, while the black jumprock South Fork 10% model may be compromised by problems of collinearity. For the Roanoke logperch, AREA is the only significant term, therefore the multiple regression models provide no additional information beyond that revealed by the univariate correlations.

Composite Model

Based on the results obtained in the previous two sections, JNCT and AREA

Combined, 50% Suitability

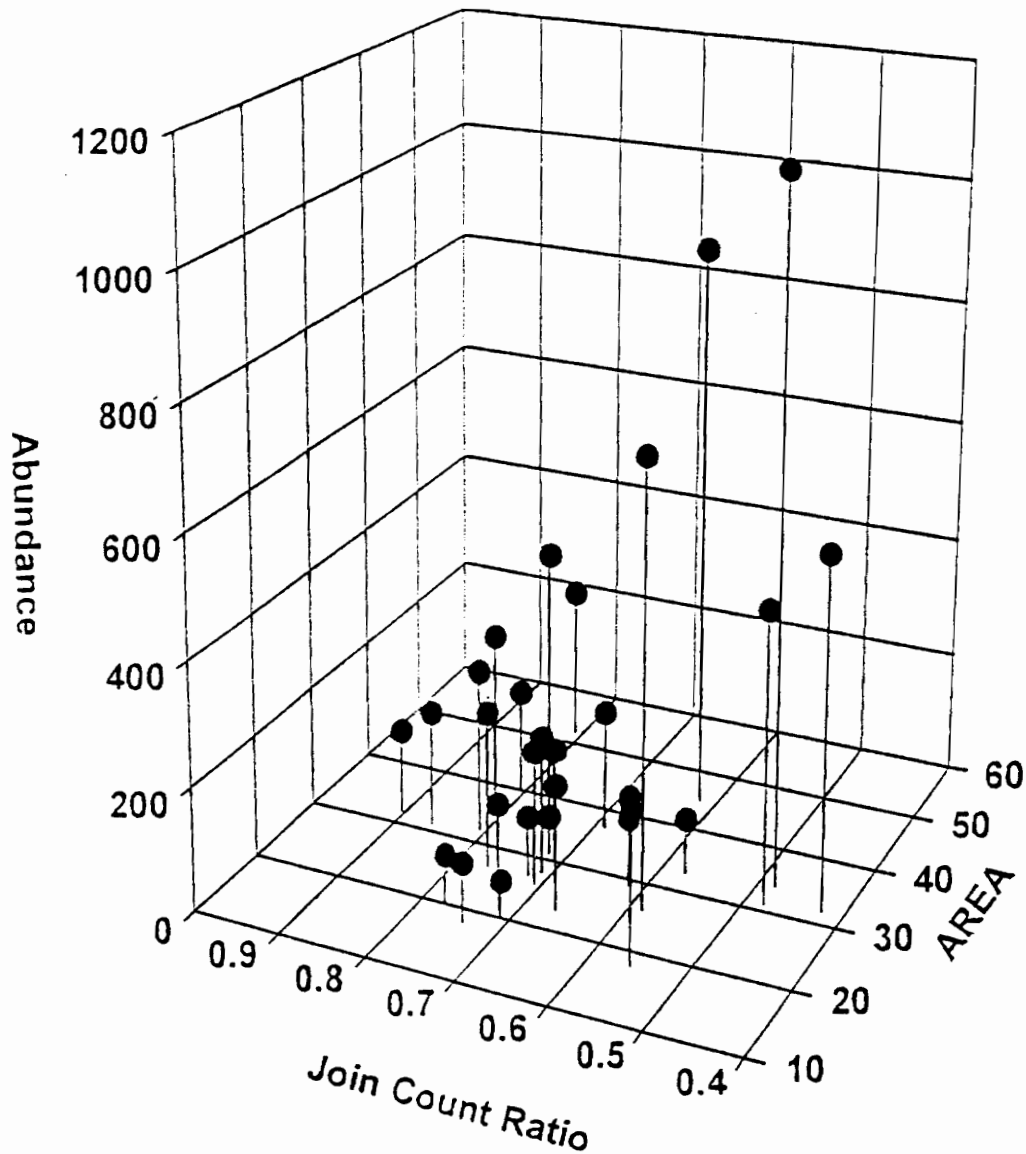
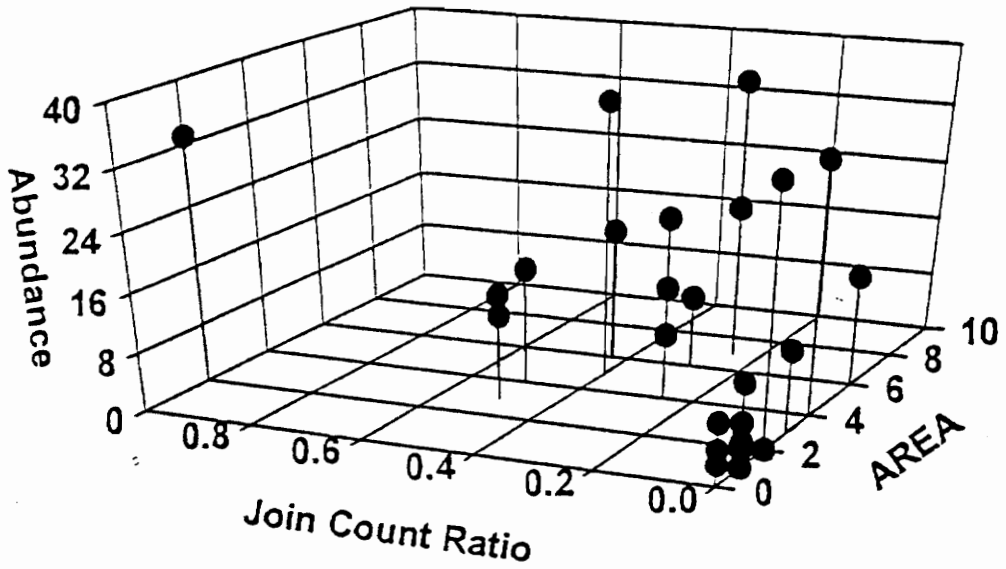


Figure 3.7. Scatterplot of Roanoke darter abundance (# of fish per site) versus both the join count ratio and area of suitable habitat for the combined data set at the 50% suitability level. The multiple regression equation quantifying the relationship among the variables is given in Table 3.4.

Combined, 5% Suitability



Roanoke, 5% Suitability

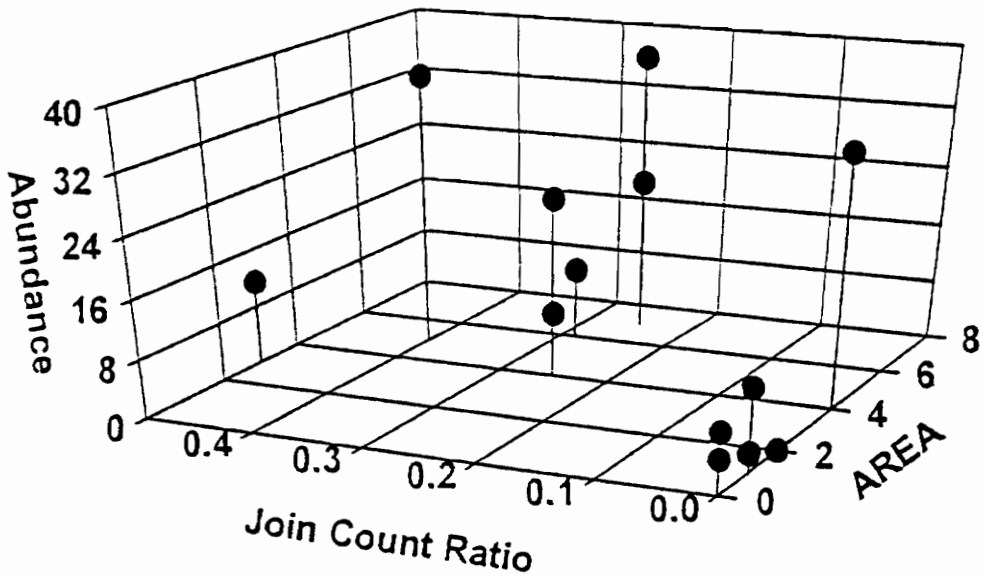
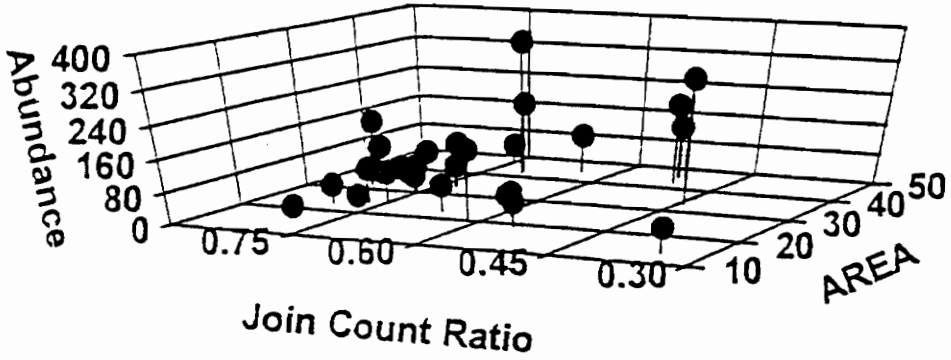
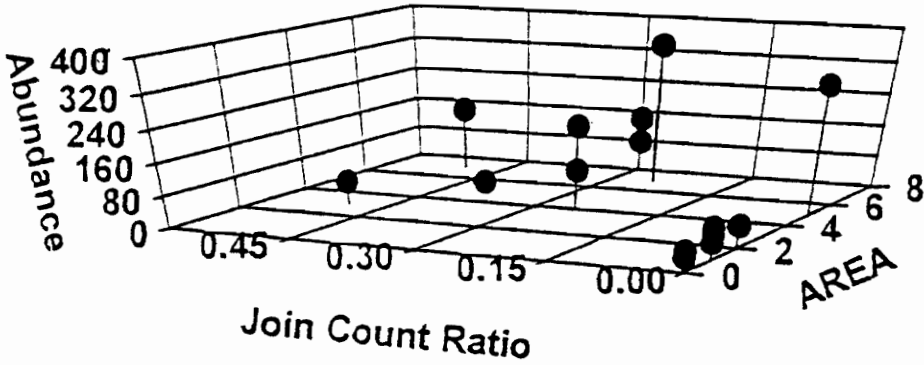


Figure 3.8. Scatterplot of Roanoke logperch abundance (# of fish per site) versus both the join count ratio and area of suitable habitat for the combined data set at the 5% suitability level and the Roanoke data set at the 5% suitability level. The multiple regression equations quantifying the relationship among the variables are given in Table 3.4.

Combined, 50% Suitability



Roanoke, 10% Suitability



South Fork, 10% Suitability

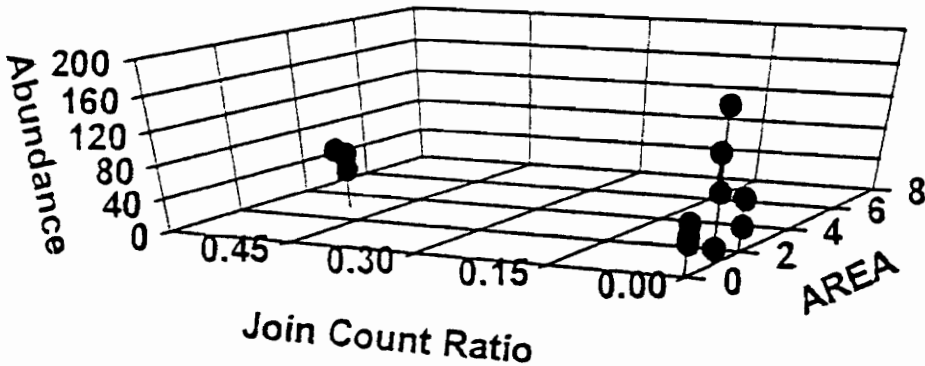


Figure 3.9. Scatterplot of black jumprock abundance (# of fish per site) versus both the join count ratio and area of suitable habitat for the combined data set at the 50% suitability level, the Roanoke data set at the 10% suitability level, and the South Fork data set at the 10% suitability level. The multiple regression equations quantifying the relationship among the variables are given in Table 3.4.

were the only two intermediate scale measures of habitat that proved to be significant in predicting fish abundance. Univariate correlations between AREA and multivariate WUA estimates from Chapter 2 were highly significant (Pearson's r , $P < 0.001$ for all three species) and inclusion of both in a multiple regression model would have resulted in problems with collinearity. Therefore, for Roanoke darter and black jumprock, I replaced AREA with WUA in the model developed in this chapter and then compared the results with the model containing AREA. Although both models were significant for both species (F-test, $P < 0.05$), the model containing AREA explained a greater portion of the variation in fish abundance than the model containing WUA for both species (33% to 26% for black jumprock, 42% to 32% for Roanoke darter). Since the JNCT term was not significant for Roanoke logperch, I simply compared the univariate correlation between AREA and abundance with that obtained for WUA and abundance in Chapter 2. Again, the model developed in this chapter served as a better predictor of fish abundance as the WUA/abundance correlation was not significant (Spearman's correlation coefficient, $P > 0.05$) but the AREA/abundance correlation was highly significant ($P < 0.001$).

Discussion

Adjacent Cell Suitability

The two landscape processes that provide the conceptual framework for my hypothesis that adjacent cell habitat will influence the density of the three study species in target cells focus on two different functions for adjacent habitat patches. Supplementation suggests that patches in close proximity to other patches providing similar resources should support higher densities of the study organism than patches that are isolated from patches providing that resource (Dunning et al. 1992). In contrast, complementation focuses on adjacent patches that share needed, but non-substitutable resources. Adjacent patches sharing these resources should support higher densities of the target organism than would be the case if either of the two

patch types occurred in isolation (Dunning et al. 1992). My results indicate that fish densities in target cells with less than optimal conditions (i. e. cells not in the upper quartile of the multivariate suitability index from Chapter 2) do vary as a function of adjacent cell habitat conditions (Figures 3.1, 3.2, and 3.3). Furthermore, habitat conditions in adjacent cell that are associated with higher densities in lower quality target cells are similar to those identified in Chapter 2 as being preferred by the 3 target species. For example, the Roanoke darter fair suitability class Kruskal-Wallis test on the PCA class combinations showed that target cells adjacent to shallow, fast cells had higher darter densities than cells adjacent to slow, deep areas. Both the univariate and multivariate habitat descriptors in Chapter 2 indicated higher densities in shallow, fast target cells. Similarly, the Kruskal-Wallis test for the Roanoke logperch fair and good suitability classes showed higher logperch densities in target cells adjacent to deep, fast areas and the Chapter 2 univariate and multivariate descriptors showed highest densities in cells with those habitat characteristics. Given these similarities between "suitable" adjacent cell habitat conditions and "suitable" target cell conditions, it seems reasonable to infer that both adjacent and target cells are providing similar resources and therefore, supplementation is occurring. If adjacent cells were providing some other type of needed resource, it seems reasonable to expect that adjacent cell conditions promoting high target cell densities would differ from characteristics identified in Chapter 2. Since there were no markedly different types of adjacent habitat that promoted higher target cell densities, the results do not support the role of complementation for adjacent cell habitat.

My results contrast with available information that indicates habitat complementation may be an important process for fish. Although the terminology used differs, much of the work on optimal foraging, predation risk, and energetic trade-offs provide explicit evidence of the importance of spatial proximity of non-

substitutable resources for fish. For example the extensive work on foraging and predation risk with creek chub (Semotilus atromaculatus) clearly demonstrates the importance of both food availability and predation refuge for this species (Fraser and Cerri 1982, Fraser 1983). It has also been demonstrated that larger armored catfish (Loricariidae) forage in shaded pools with lower algal biomass while forgoing foraging opportunities available in open canopy, algae-covered pools due to increased risk of predation from avian predators (Power et al. 1990). Likewise, central stonerollers (Campostoma anomalum) may avoid larger, deeper pools with more abundant algal mats due to the presence of predatory centrarchids to forage in predator-free areas with lower algal densities (Power and Matthews 1983, Power et al. 1985). Finally, salt marsh fishes forage preferentially in areas of tidal marshes that are in close proximity to tidal creeks pools that maintain considerable depth at low tide, again to provide predation refuge (McIvor and Odum 1988).

Complementation is also important for many rheophilic water column fishes (i. e. salmonids and cyprinids), particularly as a way of balancing food availability and the energetic demands associated with position maintenance in lotic waters. For example , schools of rosyside dace (Clinostomus funduloides) aggregate in slower, backwater eddies adjacent to higher velocity runs in Appalachian mountain streams (Freeman and Grossman 1993) as a way to maximize access to drifting invertebrates while minimizing the cost of holding position in fast water. Although slackwater areas with identical microhabitat characteristics exist in other portions of the stream, those not adjacent to high velocity water are rarely occupied by dace. Abundant evidence exists for similar behavior for many stream-dwelling salmonids (Fausch 1984, Facey and Grossman 1991).

It should be clear from the evidence presented that complementation is an important process for stream fish. It should also be clear that in those cases where it can be demonstrated, the functional significance of the adjacent (or overlapping)

resource patches is well defined. As I have already indicated, the functional significance of the preferred habitat combinations I have identified for Roanoke darter, Roanoke logperch, and black jumprock is unclear. Because of this, the approach I have used is skewed towards identification of supplementation effects. Therefore, the evidence for lack of complementation effects is weak at best.

In addition to the problems associated with a lack of clear functional significance for the habitat I have identified as optimal, there is at least one methodological factor that may have an effect on the patterns I observed. My patch size (45 m²) was defined a priori by the longitudinal and lateral spacing of measured points along my habitat transects. Ideally, patch size should be scaled based on the normal range of activity of the organism studied (Addicot et al. 1987, Wiens 1989). Again, knowledge of the normal activity range of benthic stream fish is limited, but available information on short term movements of small percids indicate that my cells are somewhat larger than the area covered by similar darters and logperch (Greenberg 1991, Freeman and Freeman 1994). Furthermore, studies of the movements of a variety of benthic riffle fish over longer time scales indicate home ranges are probably equal to if not less than a single riffle (Brown and Downhower 1982, Hill and Grossman 1987). On the other hand, based on the studies cited previously, complementation effects may occur over fairly limited spatial scales (e. g. the run/backwater complementation for rosyside dace) that are much smaller than my habitat cells. For example, it was not uncommon to see both Roanoke darter and Roanoke logperch in fast riffles and runs in low velocity water on the downstream side of large cobble or boulder substrate. If large substrate is important as a temporary "resting place" during the course of foraging, then the presence of such substrate may complement the food resources available in the faster water. Unfortunately, the coarse scale of habitat measurement does not allow me to quantify such a fine-scale phenomenon. Therefore, because of my choice of patch

size, my approach is probably biased to detection of supplementation effects.

Supplementation is a useful concept in that it refines the description of suitable habitat types in the previous chapter. However, it does not identify other potentially important types of habitat that may regulate population densities. Given that the dominant process identified by my adjacent cell analysis is supplementation, it should not be surprising that incorporation of adjacent cell effects resulted in no significant increase in the predictive capabilities of the microhabitat models.

Spatial Distribution of Suitable Habitat

The next issue to be addressed is the role of contiguity of suitable habitat in determining the ability of a riffle to support high fish abundance. The null hypothesis set out in the introduction stated that there should be no difference in fish abundance between riffles with highly contiguous, suitable habitat and riffles where suitable habitat is broken into a number of small, potentially isolated patches. My results provide evidence for rejection of the null hypothesis, however, there is also little indication that the implied alternative, i.e., that areas with highly contiguous habitat should support high fish abundances, is correct either. In fact, the results obtained for Roanoke darter and black jumrock support the interpretation that riffles with highly heterogenous habitat support the highest fish abundances.

The underlying assumption of the conceptual framework I used to develop the idea of contiguous habitat supporting higher fish densities was that movement between suitable patches would come at an associated cost, either in decreased time spent foraging or increased exposure to predation risk. In retrospect, two other possible mechanisms may also be at work in riffles. First, it may be that areas of habitat that failed to receive a suitable rating based on the Chapter 2 criterion are benign, offering neither increased benefits or risks to individuals. Second, habitat that failed to receive a suitable rating may serve other needed functions that I failed to identify based on my limited temporal sampling. If this is the case, the

complementation effects I failed to identify in the previous section may be an important consideration.

A benign habitat interpretation would result in a significant AREA effect and a non-significant JNCT effect, as the only important factor influencing population abundance is the overall availability of preferred habitat. This is the pattern that I observed for Roanoke logperch, as the species' abundance was significantly correlated with AREA for the combined data set at both the 5% and 10% suitability levels, in the Roanoke data set at the 5% suitability level, and in the South Fork data set at 10% suitability level.

In contrast, if heterogenous riffles are important, then there should be some minimal level of Chapter 2 "suitable" habitat required to meet the needs of the species, but this habitat should be interspersed with habitats containing other needed, non-substitutable resources. As the proportion of suitable habitat in a riffle increases, the availability of other habitat types declines, resulting in a riffle with high AREA and JNCT values. Since these riffles lack the other, complementary resources, they should support lower fish abundances. This is the pattern I observed for both the Roanoke darter and black jumprock in the combined 50% suitability data sets.

As I indicated in the previous section, there is direct evidence that complementation is an important process for many species of fish. However, I also argued that most of the available evidence indicates complementation occurs at spatial scales finer than the resolution of my habitat cells. Although direct evidence is not available for complementation at this scale, an indirect argument can be made that the process is important at the scale used in this section. In a study on the diel feeding chronology and habitat use of riverine fishes, Kwak et al. (1992) found that 5 different riverine fish showed marked periodicity in feeding intensity. Habitat used during feeding periods was markedly different from the types of habitat used during

non-feeding periods. Although their study did not attempt to link these differences to the population dynamics of the species or assess densities in areas lacking one of the complementary types of resources, it seems reasonable to infer that the availability of only one of the two habitat types would not be sufficient to insure the presence of the target species. Therefore, complementation is potentially applicable at larger spatial scales (i.e. riffle/run or mesohabitat scale units greater than 10^2 m) in addition to the fine scales (i.e. microhabitat scales less than 10^2 m) illustrated earlier.

One of the underlying assumptions of habitat models used by many fisheries and wildlife management agencies is that habitat units of differing suitability are exchangeable (USFWS 1980). For example, a site with a single cell with a suitability index of 1.0 and nine cells with a 0.0 suitability index receives the same WUA value as a ten-cell site where each cell has a suitability value of 0.1. It seems apparent from the results obtained here that this assumption may not be valid. If habitat units were truly exchangeable in the manner just described, then the patterns relating area of suitable habitat to fish abundance should have been robust across suitability levels. Instead, there were marked differences in explanatory power both within species across suitability levels, and across species within suitability levels.

In summary, I demonstrated that measuring habitat at intermediate scales (i.e. within a single riffle/run unit) provides information above and beyond that obtained by looking solely at microhabitat characteristics. For both Roanoke darter and black jumprock, I was able to formulate habitat models that explained a portion (admittedly small) of the variation in their abundance. Although not explicitly scale-related, the analyses show that a restrictive definition of the types of habitat that are suitable provides better predictions of logperch abundance than the WUA estimate from the previous chapter. Both supplementation and complementation appear to be important processes at this scale, but full incorporation of these concepts in future

habitat models will a require a functional approach to the assessment of microhabitat utilization and suitability.

CHAPTER 4

Large-scale habitat variables as predictors of benthic fish abundance in riffles

Introduction

In the previous chapter, I focused on both the amount and distribution of suitable habitat as an indicator of the abundance of the three study species and the manner in which habitat in adjacent areas influences the suitability of a target area. Both of these issues were addressed at a spatial scale defined by a single riffle/run unit. In this study I enlarged the scale of habitat measurement to that of discrete erosional/depositional units and investigated the way that size, spacing, and physical characteristics of these units influenced the abundance of Roanoke darter, Roanoke logperch, and black jumprock in riffles.

The two landscape processes used to frame my initial expectations in the previous chapter also apply to this larger spatial scale. An assumption underlying most of the work in this dissertation is that the availability of riffle habitat in late summer is a major factor determining abundance of Roanoke darter, Roanoke logperch, and black jumprock. This implies that riffles are suitable habitat and pools are unsuitable habitat. Not all riffles contain the same types of habitat configurations and if benthic riffle fish need multiple habitat types to meet their needs, as the results of Chapter 3 seem to indicate, then multiple types of riffles may be required to support high densities of the three study species in a given stream reach. If landscape supplementation and complementation are applicable to stream fish at the riffle/pool spatial scale, models containing variables quantifying the distribution of riffles (suitable patches) and pools (unsuitable habitat) above and below a target riffle should have some value in predicting abundance of the three study species.

This line of reasoning can be further refined by including findings from recent studies on the role of habitat fragmentation on the distribution and abundance of vertebrate populations. These models focus on the size and distribution of habitat patches and how these factors affect population density, stability, and persistence in suitable patches (Forney and Gilpin 1989, Murphy et al. 1990). They also incorporate processes that Dunning et al. (1992) term neighborhood effects. Presumably, large habitat patches provide buffering from environmental extremes and therefore complete elimination of the target species will be an uncommon event. Conversely, populations in smaller patches are more susceptible to local extinction associated with stochastic events. Although some small patches will contain populations, at any given point in time a percentage of these patches will have recently been impacted by environmental perturbation and the species either eliminated or greatly reduced. Therefore, across the universe of all small and large habitat patches, population density in large patches should, on average, be higher than population density in small patches.

A second effect of fragmentation is that proximity to adjacent patches influences densities in target patches (Fahrig and Merriam 1985, Fahrig and Paloheimo 1989, Robinson et al. 1992). Patches in close proximity to other patches will benefit from a "rescue effect" when population density has been reduced by environmental perturbations, and should therefore return to equilibrium population levels more rapidly. Conversely, isolated habitat patches will return to pre-perturbation population levels more slowly since population recovery is dependent on within-patch mechanisms. Across the universe of all available patches, patches of suitable habitat in close proximity to other suitable patches should, on average, support higher population densities than those at some distance from other patches of suitable habitat (Fahrig and Merriam 1985). Patch proximity is also likely to influence densities in linear stream systems since the effects of patch size and

spacing have been shown to be more important in systems where dispersal occurs along corridors than in systems where dispersal is random (Fahrig and Paloheimo 1989). Although fragmentation has typically been applied to situations where formerly large patches of homogenous landscape have been broken into smaller, isolated pieces (e. g. van Dorp and Opdam 1987), the processes (e. g. neighborhood effects) that produce the observed patterns should function in the patchy stream environment created by pool-riffle sequences.

Based on these ideas, three predictions relating adjacent pool-riffle characteristics to densities of riffle-dependent species were generated. The first was that fish densities in large riffles should be higher than fish densities in small riffles. The null hypothesis was that there would be no significant differences in fish density between large and small riffles. The second prediction was that riffles associated with high adjacent riffle area should have higher fish densities than riffles associated with low adjacent riffle area. The associated null hypothesis was that there were no significant differences in fish densities in riffles associated with high adjacent riffle areas than in riffles associated with low adjacent riffle areas. The final prediction was that adjacent habitat should explain a greater proportion of the variance in fish densities in smaller riffles than in larger riffles. The null hypothesis here was that the proportion of variance explained by adjacent habitat unit variables would not differ between large and small riffles. As in the previous studies, significant variables at this scale were combined with important variables from the previous studies to determine if a multi-scale model provided additional predictive power. Four objectives with management implications addressed in this chapter are to determine 1) the value of riffle size in predicting the density of the three target species, 2) the value of physical characteristics other than area of adjacent upstream and downstream pools and riffles in predicting the density of the three target species, 3) the value of the total area of pool and riffle habitat upstream and

downstream in predicting the density of the three target species, and 4) the utility of a multi-scale model in predicting density of the three target species.

Methods

Field Data Collections

Sampling for this study was carried out in Roanoke River in 1991 and in South Fork Roanoke during 1992 and 1993. In Roanoke River, sampling was conducted upstream, within, and downstream of sites RR5-RR8 described in Chapter 1. In South Fork Roanoke, four separate stream segments were sampled. The first segment (approximately 2 km in length) began 0.5 km upstream of the confluence of the North and South Fork Roanoke. The second segment extended approximately 4 km downstream of the U.S. Route 460 bridge east of Shawsville and the third segment (approximately 1.5 km long) began 1 km upstream of the same bridge. The last segment extended approximately 3.5 km upstream from the confluence of South Fork Roanoke with Elliott Creek (Figure 4.1).

Density Estimation

Counts of Roanoke darter, Roanoke logperch, and black jumprock were obtained in each of the four sites in Roanoke River in 1991 and in individual riffle/run habitat units in each of the South Fork study segments in 1992 and 1993. In the South Fork, beginning at the downstream end of each of the sampled reaches, two divers equipped with mask and snorkel walked upstream along the streambank until a riffle/run unit was encountered. The divers entered the unit at the downstream end, spaced at approximately one-third and two-thirds of the distance from the left ascending bank. The divers moved slowly upstream through the unit, keeping a tally of all Roanoke darter, Roanoke logperch, and black jumprock

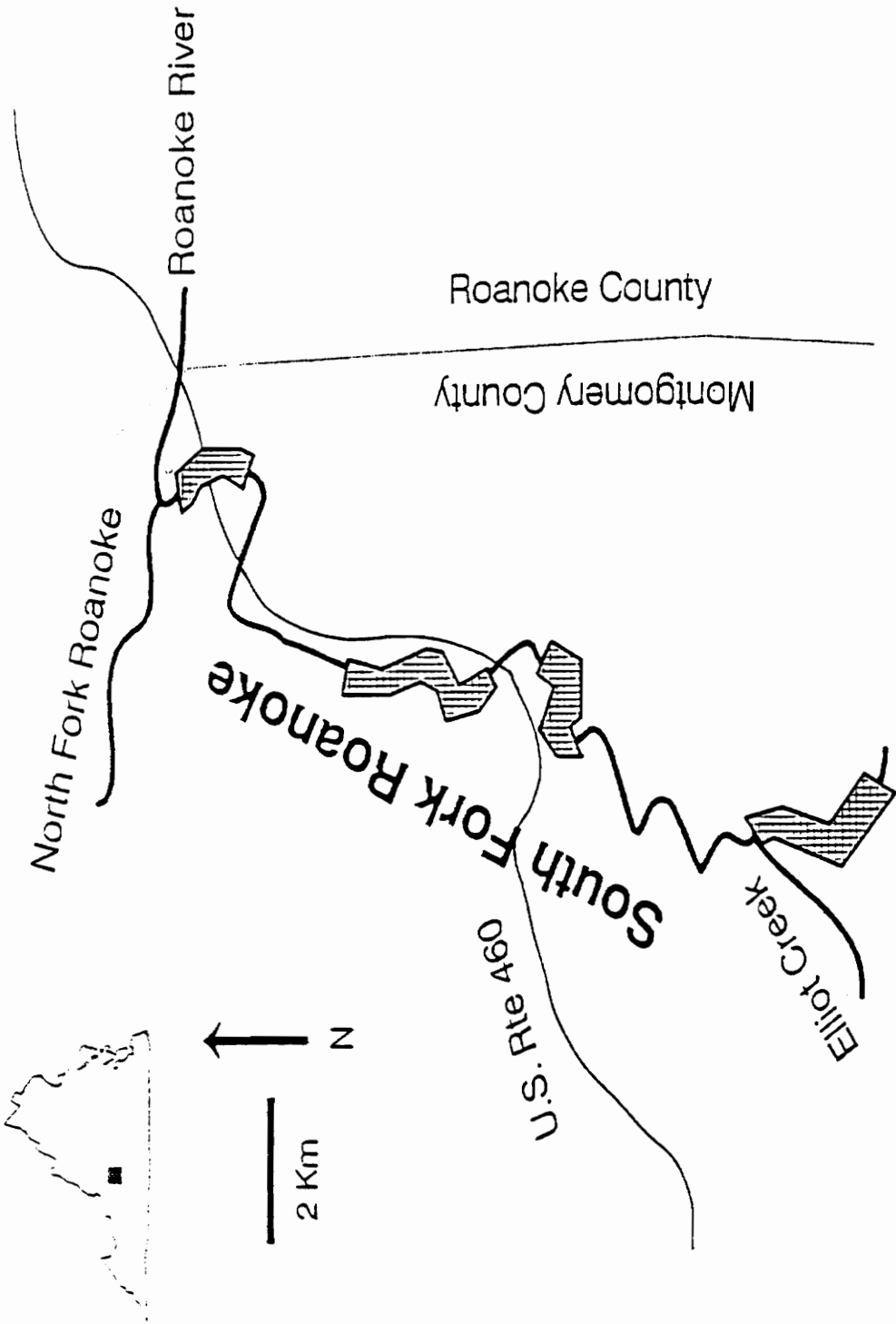


Figure 4.1. Areas sampled in South Fork Roanoke during 1992 and 1993. Hatched areas indicate reaches covered during the course of sampling.

observed. In order to minimize the possibility of double counting, divers remained abreast of each other and maintained the original spacing established at the downstream end of the riffle. Following completion of the snorkeling pass, the length of the unit was measured and unit length and the number of each species observed by each diver recorded. At the beginning and end of each day, maximum sighting distance was estimated using either a Secchi disk or by taking a turbidity measurement. Densities of the three target species in each of the individual riffle/run units were estimated using the Emlen technique described in Chapter 1.

Habitat Measurements

Following completion of underwater observation passes, I measured large scale habitat characteristics upstream and downstream of the snorkeled riffles. In each of the sampled reaches, habitat measurement began in the first riffle or pool whose upstream end began at least 250 m from the downstream end of the first riffle-run unit snorkeled. In each of the riffles and pools within the sampled reaches, habitat measurements were taken along at least two transects located systematically through the unit being measured. On each transect, measurements were taken at three points, located at one-quarter, one-half, and three-quarters of the total length of the transect. At each point, water depth, dominant substrate, and subdominant substrate were recorded, and an ordinal-scale measure of water velocity was obtained. In 1992, an attempt was made to obtain exact velocity measurements at each point using a current meter, but this proved to be too time-consuming. In order to allow me to sample enough units to obtain a reasonable sample size, I visually assessed current velocity as either slow, moderate, or fast. In order to validate the accuracy of my visual assessment, during the course of the microhabitat sampling carried out for Chapter 2 during 1993, I visually classified velocities at sampled microhabitat points where current velocity was actually measured. Points classified

as low velocity ranged from 0 to 18 cm/s, those classified as moderate velocity ranged from 15 to 46 cm/s, and those classified as high velocity ranged from 39 to greater than 100 cm/s. Although there was overlap between measured and visually classified velocities, I felt the increased sample size obtained by using this technique was worth the cost of decreased precision. Furthermore, I was the only person quantifying velocity, so errors should have been consistent across sampled units. In addition to the habitat measures taken at each of the points, stream width was measured at each transect. The total length of each unit also was recorded.

Statistical Analysis

To examine the relationship between riffle size and fish density, all riffles snorkeled during 1991, 1992, and 1993 were classified into one of three groups based on surface area. Since the distribution of riffle surface area was unimodal, the three groups were established by dividing the total data set into groups with equal sample sizes. The surface area of the three classes were $< 925 \text{ m}^2$ (small riffles), $\geq 925 \text{ m}^2$ and $< 1675 \text{ m}^2$ (medium riffles), and $> 1675 \text{ m}^2$ (large riffles). For each of the three species, a Kruskal-Wallis test was used to determine if there were significant differences in density among the three riffle class.

To examine the value of adjacent habitat unit characteristics in predicting fish density, two sets of variables quantifying adjacent unit habitat were developed. The first set addressed the total area of pool (TPARE) and riffle (TRARE) habitat upstream and downstream of the sampled units. For this data set, the total area of pool and riffle habitat 250 m upstream and 250 m downstream of the target riffle were calculated. For the purposes of this analysis, if the upstream end of a downstream pool or riffle began less than 250 m downstream from the downstream end of the target riffle, the total area of that unit was included in the downstream total for that type of unit. Conversely, if the downstream end of an upstream pool or

riffle began within 250 m of the upstream end of the target riffle, the total area for that unit was included in upstream total for that unit type. Unit areas were estimated by multiplying the width for that unit (estimated by averaging the measured widths from the habitat transects) by the total length of the unit.

The second set of variables quantifies the types of riffles and pools immediately adjacent to the target riffle (i.e., the first pool and riffle upstream and downstream from the target riffle). The raw data for this set of variables were drawn from the depth, velocity, and substrate measurements obtained from the habitat transects. For both pool and riffle units, three separate measures of the types of habitat available were developed. Measures of mean pool depth (PDEP) and mean riffle depth (RDEP) were obtained by averaging the depth measurements in adjacent upstream and downstream riffles, respectively. Likewise, indices of pool current velocity (PVEL) and riffle current velocity (RVEL) were obtained by averaging the categorical measures of velocity obtained in upstream and downstream pools and riffles, respectively. Finally, indices of pool substrate coarseness (PSUB) and riffle substrate coarseness (RSUB) were estimated. For the substrate scores, dominant and subdominant substrate were collapsed into the same three category classification as in the previous two chapters and the upstream and downstream pool and riffle scores averaged, respectively.

The first step in determining the value of each of the 8 habitat variables in predicting fish density was to inspect box plots for each of the variables and for densities of each of the three species to determine potential outliers. Extreme outliers (points removed more than three interquartile ranges from the 25th or 75th percentiles (Tukey 1977)) were eliminated from the data set. This resulted in the elimination of three target riffles for Roanoke darter and Roanoke logperch and two target riffles for black jumprock.

Following elimination of outliers, the relationship between fish density and

(Spearman's correlation coefficient) and multiple regression analysis. For the multiple regression analysis, all variables were initially entered and then backward elimination used to eliminate those variables not contributing significantly to the overall model. Variables were retained if the individual contribution was significant at $P < 0.15$. In addition to carrying out the correlation and regression analyses on the full data set, the relationship between adjacent unit habitat and riffle size was examined by conducting the same analyses on reduced data sets composed of small, medium and large riffles.

To determine the utility of combining variables across all three measurement scales, I again used multiple regression analysis with a backward variable selection procedure. Habitat measurements at all three spatial scales and fish abundance estimates were available for four Roanoke River sites shocked in 1991 (Sites RR5-RR8), six South Fork sites shocked in 1992 (SF1-SF4, SF7 and SF8), and five South Fork sites shocked in 1993 (SF1-SF3, SF7 and SF8). All significant variables from both the current and previous chapters were initially entered into the regression model and the least significant variable was eliminated until all remaining variables were significant ($P < 0.15$). As noted in the last chapter, estimates of AREA from Chapter 3 and multivariate WUA from Chapter 2 are highly correlated, so if both of these variables had been shown to be significant two separate regression analyses were conducted with only one of these two in the initial variable list.

Results

Riffle Size and Fish Density

Median densities of Roanoke darter in small, medium, and large riffles were $1640 \cdot \text{ha}^{-1}$, $1630 \cdot \text{ha}^{-1}$, and $1827 \cdot \text{ha}^{-1}$, respectively (Figure 4.1). Differences between riffle size classes were not significant ($P > .05$). For Roanoke logperch, median densities were $54 \cdot \text{ha}^{-1}$, $28 \cdot \text{ha}^{-1}$, and $13 \cdot \text{ha}^{-1}$ in small, medium and large riffles,

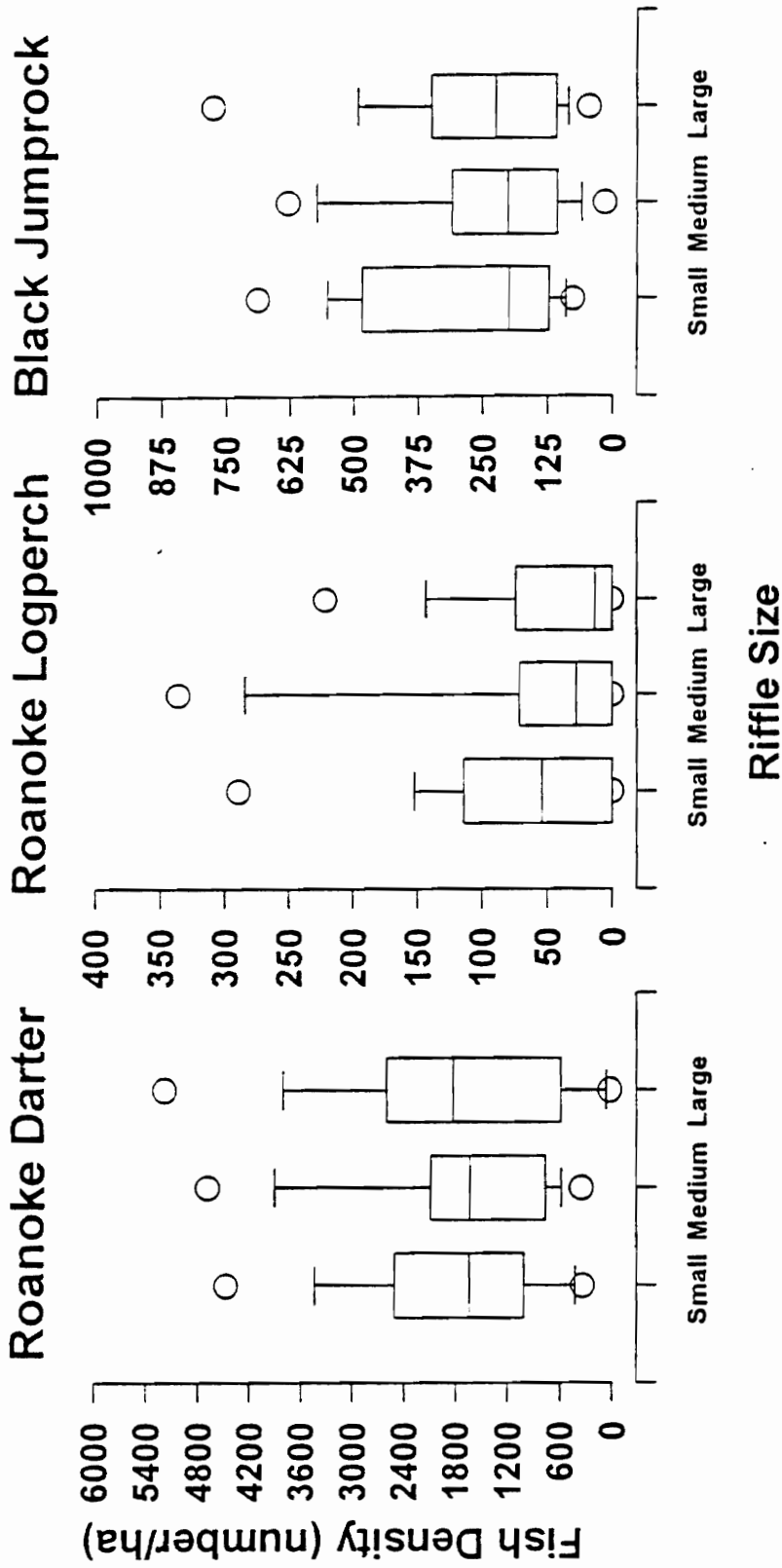


Figure 4.2. Box plots of Roanoke darter, Roanoke logperch, and black jumprock densities in small, medium, and large riffles. The box encloses the middle 50% of observations, the capped vertical bars extend to the 10th and 95th percentiles, the open circles represent the 5% and 95% percentiles, and the horizontal bar in the box represents the median.

respectively (Figure 4.1). Although there was a trend towards higher densities in small riffles and lower densities in large riffles, the differences were not significant ($P > .05$). Black jumprock median densities were $199 \cdot \text{ha}^{-1}$ in small riffles, $181 \cdot \text{ha}^{-1}$ in medium riffles, and $224 \cdot \text{ha}^{-1}$ in large riffles (Figure 4.1). Again, differences among riffle size classes were not significant ($P > .05$).

Adjacent Unit Habitat Variables and Fish Density

There were no significant univariate correlations between Roanoke darter density and any of the 8 macrohabitat variables for either the full data set or any of the reduced data sets (Table 4.1). For Roanoke logperch, fish density was positively correlated with total pool area for all data sets, except in medium riffles, and positively correlated with riffle depth in the full data set. Logperch density was negatively correlated with total riffle area in both the full and small riffle data set (Table 4.1). Total pool area was positively correlated with black jumprock abundance in the full and medium riffle data sets, while total riffle area was negatively correlated with black jumprock density in the full data set (Table 4.1).

Significant multiple regression models relating Roanoke darter density to at least one of the eight macrohabitat variables were obtained for all four data sets (Table 4.2). The proportion of density variation explained by the models ranged from 29% for the full model to 68% for the large riffle model. Variance explained in the reduced data sets increased with increased riffle size. Although different variables were retained by the backward selection procedure for the 4 models, the coefficient signs of those variables appearing in more than one model were consistent. Darter density was always negatively associated with pool velocity and total riffle area and positively associated with pool substrate in those models where the variables were included.

There was no significant model relating logperch abundance to macrohabitat

Table 4.1. Correlation coefficients (Spearman's ρ) between fish densities in individual riffles and macrohabitat variables for the entire data set, and for 3 subsets based on riffle size. P-values are given in parentheses for significant correlations ($P < 0.05$.)

Data Set	Pool Area	Riffle Area	Pool Depth	Pool Velocity	Pool Substrate	Riffle Depth	Riffle Velocity	Riffle Substrate
Roanoke Darter								
All n=45	-0.108	-0.003	-0.171	-0.035	0.213	0.021	0.049	0.126
Small n=17	-0.265	0.346	-0.302	0.112	0.115	0.189	0.064	0.069
Medium n=16	0.421	-0.026	0.171	-0.077	0.412	0.032	0.192	0.280
Large n=12	-0.429	-0.330	-0.555	-0.099	0.289	-0.115	-0.038	0.185
Roanoke Logperch								
All n=45	0.560 ($< .001$)	-0.408 (.005)	0.156	0.087	-0.214	0.301 (.045)	0.039	-0.137
Small n=17	0.601 (.011)	-0.526 (.030)	0.292	-0.102	-0.247	0.219	-0.351	-0.247
Medium n=16	0.418	-0.251	0.112	-0.051	-0.368	0.165	0.381	-0.015
Large n=12	0.595 (.041)	-0.225	0.268	0.412	0.080	0.551	0.000	-0.531
Black Junprock								
All n=46	0.312 (.033)	-0.293 (.046)	-0.150	0.025	-0.033	0.188	-0.031	-0.020
Small n=17	0.376	-0.340	-0.174	-0.090	-0.037	0.082	-0.323	0.076
Medium n=16	0.521 (.039)	-0.414	0.365	-0.038	-0.235	0.279	0.165	0.112
Large n=13	0.108	-0.121	-0.226	0.022	-0.066	0.235	0.015	-0.236

Table 4.2. Significant regression models accounting for the greatest variance in Roanoke darter densities for the full data set and for reduced data sets based on the size of the target riffle. Abbreviations are PDEP = Pool depth, PVEL = Pool velocity, PSUB = Pool substrate, RSUB = Riffle substrate, TRARE = Total riffle area.

Data set	Model	Significance (<i>P</i>)		<i>R</i> ²
		Coefficient	Model	
All	Density = 4279.546	0.020	0.003	0.285
	-32.269 PDEP	0.023		
	-3638.858 PVEL	0.006		
	+2270.058 PSUB	0.002		
Small	Density = -53.978	0.938	0.009	0.376
	-0.415 TRARE	0.009		
Medium	Density = -622.250	0.851	0.020	0.625
	-46.168 PDEP	0.064		
	-7736.153 PVEL	0.006		
	+4405.339 PSUB	0.003		
	+2705.446 RSUB	0.048		
Large	Density = 643.764	0.766	0.012	0.684
	-0.713 TRARE	0.005		
	-5184.827 PVEL	0.011		
	+6472.179 PSUB	0.004		

There was no significant model relating logperch abundance to macrohabitat variables for the small riffle data set, but models for the other 3 data sets were all significant (Table 4.3). The proportion of density variance explained for the significant models ranged from 30% for the full data set to 74% for the medium riffle data set. Total pool area was positively associated with logperch density in all the significant models, while high logperch densities were positively associated with shallow, slow pools and deep, coarse-bottomed riffles in the medium riffle data set.

The only significant macrohabitat model for black jumprock came from the medium riffle data set and explained 69% of the variation in jumprock density (Table 4.4). Jumprock density was negatively associated with total riffle area, pool depth, pool substrate, and riffle velocity and positively associated with riffle depth. Although the full model approached significance ($P = 0.068$), it explained only 7% of the variance in jumprock density.

Combined Models

Variables initially entered into the multiple regression analysis for Roanoke darter were AREA and JNCT from the 50% suitability data set (Chapter 3) and total riffle area, pool depth, pool substrate, riffle depth, and riffle velocity. Total riffle area, pool depth, and pool substrate were the only variables retained and the final model explained 58% of the variation in darter abundance at the 15 sites (Table 4.5). For Roanoke logperch, both WUA (Chapter 2) and AREA at the 5% suitability level (Chapter 3) were significant, so two separate models were developed with the initial variable list containing only one of the two. Other variables included were total pool area, pool depth, pool velocity, pool substrate, riffle depth, and riffle substrate. The only significant model related abundance to WUA and explained only 37% of the variance in logperch abundance (Table 4.5). For black jumprock, AREA and JNCT from the 50% suitability level (Chapter 3), total riffle area, pool depth, pool substrate, riffle depth, and riffle velocity were entered into the initial regression

Table 4.3. Significant regression models accounting for the greatest variance in Roanoke logperch densities for the full data set and for reduced data sets based on the size of the target riffle. Abbreviations are TPARE = total pool area, PSUB = pool substrate, PDEP = pool depth, PVEL = pool velocity, RDEP = riffle depth, RVEL = riffle velocity.

Data set	Model	Significance (<i>P</i>)		<i>R</i> ²
		Coefficient	Model	
All	Density = 94.510	0.196	< 0.001	0.302
	+0.020 TPARE	< 0.001		
	-79.154 PSUB	0.056		
Small		No Significant Model		
Medium	Density = 27.774	0.919	0.010	0.740
	+0.039 TPARE	0.001		
	-5.250 PDEP	0.031		
	-445.002 PVEL	0.015		
	+7.387 RDEP	0.088		
+188.225 RSUB	0.098			
Large	Density = -29.369	0.470	0.047	0.339
	+0.028 TPARE	0.047		

Table 4.4. Significant regression models accounting for the greatest variance in black jumprock densities for the full data set and for reduced data sets based on the size of the target rifle. Abbreviations are TRARE = total rifle area, PDEP = pool depth, PSUB = pool substrate, RDEP = rifle depth, RVEL = rifle velocity.

Data set	Model	Significance (<i>P</i>)		<i>R</i> ²
		Coefficient	Model	
All	Density = 408.729 -0.032 TRARE	< 0.001 0.063	0.063	0.074
Small		No Significant Model		
Medium	Density = 1585.486 -0.133 TRARE -7.359 PDEP -225.921 PSUB +27.521 RDEP -311.436 RVEL	0.015 0.003 0.061 0.114 0.004 0.125	0.021	0.692
Large		No Significant Model		

Table 4.5. Significant multi-scale multiple regression models accounting for the greatest variance in Roanoke darter, Roanoke logperch, and black jumprock abundance (number of fish per site) for the for 15 electroshocking sites sampled in the Roanoke River in 1991 and the South Fork Roanoke in 1992 and 1993. Abbreviations are TRARE = total riffle area, PDEP = pool depth, RSUB = riffle substrate, RVEL = riffle velocity, MVWUA = weighted usable area using the multivariate suitability index, and AREA50 = area of suitable habitat using the 50% suitability criteria.

Species	Significance (<i>P</i>)			<i>R</i> ²
	Model	Coefficient	Model	
Roanoke Darter	Abundance = 359,008	0.037	0.018	0.583
	+0.013 TRARE	0.081		
	+1.435 PDEP -143.995 RSUB	0.074 0.024		
Roanoke Logperch	Abundance = -9,981	0.254	0.015	0.374
	+1.181 MVWUA	0.015		
Black Jumprock	Abundance = 444,967	0.014	0.013	0.610
	+8.453 AREA50	0.003		
	-0.019 TRARE -210.199 RVEL	0.050 0.009		

model. AREA, total riffle area, and riffle velocity were retained in a final model that explained 61 % of the variation in jumprock abundance (Table 4.5). In summary, the model for the black jumprock was the only one including variables from more than one scale of measurement.

Discussion

The conceptual model presented in the introduction to this chapter posits that the abundance of Roanoke darter, Roanoke logperch, and black jumprock in target riffles should be a function of the size and distribution of suitable habitat patches, where suitable habitat patches were defined as upstream and downstream riffles sampled under summer low-flow conditions. The data presented above provides, at best, marginal support for the conceptual model. However, I would argue that the failure of the model results not from a poorly formulated framework, but from the assumption that availability and distribution of riffle habitat during summer is a reasonable definition of what a patch of habitat may be for these species. In the discussion that follows, I will address each of the testable hypotheses presented in the introduction and attempt to show how redefinition of the term "suitable habitat patch" may provide research avenues that would ultimately provide support for the overall conceptual framework. Expansion of the spatial scale of measurement, looking at the term proximity in a slightly different sense, or consideration of differences in the life history strategies and vagility of the three species are all potentially important considerations in this regard.

Riffle Size and Fish Density

The first prediction was that fish densities in large riffles would be higher than fish densities in smaller riffles. For all three species, there were no significant differences in fish densities among small, medium, or large riffles. In fact, the only discernible trend in the data was a tendency for logperch densities to be higher in

smaller riffles than in larger riffles. Therefore, the null hypothesis of no difference in densities among riffle sizes cannot be rejected.

My first hypothesis implicitly assumes that the short term dynamics of populations in individual riffles, particularly birth and death processes, are affected almost exclusively by intra-patch factors. Spacing, location, and type of adjacent patches become important only on longer time scales, when patch populations are reduced or eliminated by stochastic events and reestablishment or supplementation of that patch's population depends on immigration from adjacent patches (Leigh 1981, Goodman 1987, Quinn and Hastings 1987, Forney and Gilpin 1989). If movement between riffles is relatively common, then intra-patch factors are less germane and the importance of long-term extinction or population reduction within a patch declines, making the predictions generated by my framework invalid. Given that I was unable to demonstrate that riffle size alone is a factor determining fish abundance, short-term movements among patches are probably important. Furthermore, my estimates of the number of logperch or jumprock in a single riffle are well below the number of individuals necessary to maintain viable ecological metapopulations.

In Chapter 2, I argued that my cell sizes were sufficient to encompass the area used by the study species during the course of daily activities. The area used by these species over the course of their life is probably much larger, although there is currently little agreement as to how large that area might be. Earlier work on movements and home range suggested that most fish used a single pool, riffle, or pool/riffle sequence during the course of their life (Funk 1957, Gerking 1957, Hill and Grossman 1987). Recent studies have called this "limited movement paradigm" into question and suggest stream fish may be much more vagile (Riley et al. 1992). Furthermore, in a recent study of fish recolonization of a reach of the South Fork defaunated by a manure spill, there was circumstantial evidence that adult Roanoke

darther, Roanoke logperch, and black jumprock moved extensive distances (up to 4 km) in the 8 to 22 months following the disturbance (Ensign et al. in press). Increasing ease and frequency of movement among patches decreases population subdivision and consequently, makes extinction/recolonization processes virtually meaningless in intra-patch population dynamics. This would appear to be the situation for the three study species in the Roanoke and South Fork Roanoke rivers. Increased movement between riffles also shifts the emphasis of the other landscape processes used to develop the conceptual framework for this chapter from those that inhibit movement over long temporal scales to those that facilitate movement and blur the distinction between riffles over shorter time periods. This shift in emphasis will be explored further in the next section.

Spatial Proximity of Patches, Patch Size, and Fish Density

The second and third hypotheses address the importance of spatial proximity of suitable habitat in determining fish densities in the target riffles and the effect that target riffle size has on the importance of adjacent habitat. The second null hypothesis was that there would be no difference in fish densities in riffles associated with high adjacent riffle areas and in riffles associated with low adjacent riffle areas. The alternative was that high adjacent riffle area would lead to higher target riffle densities. The third null hypothesis was that there would be no relationship between riffle size and the importance of adjacent riffle habitat, with the alternative that adjacent habitat would be more important for small riffles than for large riffles. My results not only fail to indicate that the second null hypothesis should be rejected, but that for two of the three species (Roanoke darter and black jumprock) densities were negatively correlated with adjacent riffle area for at least one of the significant models. For Roanoke logperch, there was no apparent relationship between adjacent riffle area and densities, but logperch densities were positively related to adjacent pool areas. My results also fail to provide evidence to

reject the third null hypothesis, with the Roanoke darter results showing a pattern in direct opposition to that proposed in the alternative.

As I noted in the previous section, all of my predictions are based on the assumption that a single riffle is the operative unit for considering the short-term population dynamics of the study species. Furthermore, my predictions assume that the intervening habitat types (in this case, pools) are either benign or inhospitable. My results indicate that the assumptions may be badly flawed.

If pools are not inhospitable and riffles are not single, isolated functional units for the interplay of birth and death processes that set population abundance levels for the three study species, is it possible to develop a conceptual model at the habitat unit scale that incorporates elements of the landscape processes I initially postulated (i. e. supplementation, complementation, and neighborhood effects)? Based on the results obtained in this chapter and information in the literature on the life history requirements of percids and catostomids, I would argue that the answer is yes.

In developing that argument, the first step is to recognize that, despite my initial assumption, summer riffle habitat may not be the most important factor limiting population abundance of the three species. Most stream fish (including catostomids and percids) exhibit a complex life cycle (Wilbur 1980, Schlosser 1991), with different life stages requiring markedly different resource types. The size of a given cohort may be set at a number of different points including egg deposition, fry swim-up, larval/juvenile metamorphosis, first year overwinter survival, or even adult survivorship. In a variable environment, the critical life stage may differ from one year to the next, or even seasonally within a given year. Therefore, the next step is to identify what other types of resources may be needed by other life stages of the three study species.

Although all three species use riffles for spawning in the spring, studies on

other percids and catostomids indicate a high probability that there is a period of passive drift immediately following hatching that ultimately carries larvae into pools (Floyd et al. 1984). Although information is lacking for suckers, percids may spend a significant portion of their first year foraging in pools (Greenberg and Stiles 1993, Jenkins and Burkhead 1994). In addition, pool habitat has also been shown to be important over-winter refuge habitat for a variety of stream fish (Burkhead 1983, Jenkins and Burkhead 1994). Therefore, the only life stages and seasons that Roanoke darter, Roanoke logperch, and black jumprock do not require pool habitat are for spawning and foraging adults in spring and foraging adults in summer and fall. Given this information, the simplistic assumption of riffle hospitality and pool inhospitality is untenable. Instead, the stream channel takes on a much more complex functional structure, with patchy distributions of resources on both spatial and temporal scales potentially influencing the dynamics of the three study species. Although my initial hypothesis fails to take the complex patchiness of the stream environment into consideration, my results allow identification of potentially important relationships between fish abundance and the types of habitat available above and below target riffles. These findings can be used to redefine the types of patches important to the three species and provide guidance for future research on their habitat relationships.

For Roanoke darter, although there were no significant univariate correlations, the multiple regression analysis showed negative relationships between pool velocity and darter abundance and positive relationships between pool substrate coarseness and darter abundance in three of four models. Furthermore, two of four multiple regression models showed a negative relationship between pool depth and darter abundance. Greenberg and Stiles (1993) found a variety of young-of-year darters foraging over coarse substrate in slow pools during summer in Little River, Tennessee. As mentioned earlier, predatory fish are thought to have a significant

impact on habitat selection of many small stream fish, and most predatory fish forage more efficiently in deeper water (Schlosser 1987, Schlosser 1988, Angermeier 1992). Combining this information, Roanoke darter abundance is higher in riffles adjacent to pools that provide both high quality foraging areas and reduced predation pressure for young-of-year darters.

For Roanoke logperch, the only consistent pattern that emerged from both the univariate correlations and the multiple regression models was the positive relationship between logperch abundance and total pool area. Although an argument similar to that proposed for Roanoke darter is initially attractive, the lack of relationships between logperch abundance and other pool-related variables makes such an inference tenuous. A more parsimonious explanation, and one based on at least some empirical evidence (Burkhead 1983, Jenkins and Burkhead 1994), is that large pool areas provide important overwintering habitat for adult logperch.

The results for black jumprock are more difficult to interpret. Although the pattern observed in medium riffles is similar to that for Roanoke darter and Roanoke logperch, the failure to identify significant relationships in any of the other data sets suggests the results are not robust. The lack of strong large-scale habitat relationships for jumprock are most likely a function of the differences in vagility between the sucker and the two percids. Many catostomids undertake extensive pre-spawning and post-spawning migrations (Jenkins and Burkhead 1994), while percids are thought to be somewhat less mobile (Page 1983, Kuehne and Barbour 1984). If jumprock exhibit this familial tendency to roam, the spatial scale employed in this study (500 m surrounding the target riffle) may not be sufficient to characterize the large scale habitat requirements of the species.

The differences in postulated adjacent habitat function for Roanoke darter and Roanoke logperch fit well with an argument that I have advanced earlier, specifically that the types of habitat that prove to be important to these species should show

some linkages with their differing life history patterns. I placed Roanoke darter on the opportunistic end of the opportunistic-periodic continuum (Winemiller and Rose 1992) and this suggests that habitat factors facilitating juvenile survival should be important to this species. In contrast, Roanoke logperch is on the periodic end of the continuum, therefore habitat factors promoting growth and survival of adults should be important. The data in this chapter support such an inference.

In summary, further research into the large-scale habitat relationships of these three species, and most other stream fish for that matter, should explicitly recognize the varying habitat requirements associated with their complex life cycles. For opportunistic species such as the Roanoke darter, factors promoting survival of early life stages will probably be of greater importance than habitat associations of later life stages. For periodic species such as the Roanoke logperch, factors associated with growth and survival of adults will probably be more important. Therefore, a hypothesis useful for framing future studies is that availability of habitat needed by early life stages should determine the population dynamics of opportunistic strategists, while population dynamics of periodic strategists should be determined by the availability of habitat needed by adult life stages. There is no clear evidence supporting a focus on any particular habitats or life stages for the black jumprock, but a reasonable first step would be to determine the spatial extent of a stream reach used by this species during the course of its life.

Composite Model

The results obtained for the combined models suggest that the concept underlying this dissertation, i.e., that habitat measured at multiple scales should provide better predictions of fish abundance than habitat measured at any single scale, was wrong for two of the three study species. For both Roanoke darter and Roanoke logperch, the retained variables came from a single spatial scale while for black jumprock, both intermediate and large-scale variables were retained. Although

information from multiple habitat scales did not provide better abundance predictions for the two percids, the results do support my earlier arguments that life history characteristics may be important in defining the types of habitat that potentially limit populations of periodic and opportunistic strategists. Although information from multiple scales was entered into the initial models for both the darter and logperch, those factors ostensibly affecting larval and juvenile survival were retained for the former species and factors ostensibly affecting adult survival were retained for the latter. The jumprock results are less clear-cut, but the fact that variables from multiple habitat scales provided better predictions of jumprock abundance than variables from any individual scale could be related to the sucker's vagility.

The composite model results should be viewed with some scepticism given the small sample sizes and limited range of variable values from the large-scale data set. All but four of the 15 riffles used were classified as large riffles and 11 of the 15 riffles had total pool and riffle areas in the upper quartile of values used to develop the large-scale models. Therefore, potential interactions between microhabitat and intermediate habitat scale site quality measures and the large scale factors identified as important in this chapter are not fully taken into account by the final composite models. This also highlights the difficulty of attempting to develop multiple-scale models, since the time and effort needed to obtain sufficient numbers of sites where attributes at all three scale have been measured may be prohibitive.

In summary, given their low predictive capability, the multiple-scale models I developed have little immediate practical significance to management agencies. However, the techniques used may have applicability to reconnaissance-level surveys with species where little is known about habitat needs or life-history requirements. Rather than assuming that a given life-stage or habitat type limits a population, multiple-scale sampling can be used to identify those stages or habitat types that merit additional attention. This can be particularly important for special concern

species that require immediate attention due to impending anthropogenic impacts.

Summary and Management Implications

I had two overall goals in this dissertation. The first was to develop underwater observation methods for assessing the abundance of benthic riffle fishes. The second was to assess the use of multiple-scale measures of habitat availability for predicting the distribution and abundance of Roanoke darter, Roanoke logperch, and black jumprock. The evidence I presented in the preceding chapters indicates that I successfully accomplished my first goal, while my success in the second case is subject to debate.

Underwater observation has been shown to be an effective method of estimating the abundance of a variety of stream fish, but its applicability to small benthic species has been subject to question. This was primarily due to the cryptic nature of these species. I was able to show that standard strip transect models commonly used by stream fish biologists underestimate the density of benthic fishes because they fail to account for the decreased probability of sighting with increasing distance of the target individual from the observer. Estimators incorporating a correction factor that account for decreased sighting probability (i.e. the distance sampling models proposed by Emlen (1972) and Burnham et al. (1992)) provided abundance estimates that were highly correlated with both strip transect estimates and estimates based on a different gear type.

Although I lacked absolute abundance estimates that would have allowed me to assess the accuracy of the distance estimates, my results suggest that distance sampling models are a fertile area for future research. Furthermore, underwater observation has great potential for assessment of the distribution and abundance of special concern species. Increasing concern about the potentially deleterious effects of electrofishing on fish populations will place greater emphasis on non-invasive, non-destructive sampling methods. In addition, underwater observation allows much more extensive spatial and temporal sampling of populations than the catch per unit effort, depletion, and mark-recapture techniques presently used by fish biologists. Larger sample sizes mean

increased precision in statistical techniques and more robust inferences about the factors affecting stream fish populations. In summary, underwater observation works well for these species and deserves additional research.

The second goal was to develop multi-scale habitat models for Roanoke darter, Roanoke logperch, and black jumprock that could be used by fish managers to predict the abundance and distribution of these three species. My assumption was that since fish display complex life-histories and use multiple habitat types during the course of their development, sampling multiple habitat scales should have provided better predictions of abundance than samples obtained from a single measurement scale. I constrained my sampling to data that could be reasonably collected by a state or federal management biologist. Although all three species showed evidence of habitat preference or habitat selection for at least one of the three spatial scales employed, neither the models developed from the individual scales nor the multiple scale models incorporating data from all spatial scales were capable of predicting fish abundance with much precision or accuracy. In this sense, I failed to achieve my second goal.

The failure of the various habitat models highlights the limited understanding we have of the functional significance of various combinations of depth, velocity, and substrate or the how the distribution of these components at larger spatial scales determine the population dynamics of benthic riffle fishes. Successful future application of a habitat-based approach for determining potential impacts of anthropogenic activities on populations of these types of fishes will depend on our ability to effectively define the functional significance of various habitat configurations in the population dynamics of the target species.

Although I failed to develop management level models in this dissertation, my results indicate that a multi-scale approach to habitat needs assessment can provide useful information not available by sampling any single scale. For example, the two percids I studied are both benthic insectivores occurring in riffle-run habitat and both

use similar substrate types for spawning. Because of these similarities, they are often placed in similar resource-use guilds and should respond in like fashion to habitat alterations. In contrast, they occupy different points on the opportunistic-periodic life history axis of Winemiller and Rose (1991). My results indicate that the types of resources important in the population dynamics are more closely related to the differences in life-history characteristics than the similarities in resource-use guilds. My ability to make this inference is a direct function of the multiple habitat scales that I sampled.

Data collected at the largest spatial scale sampled indicated that Roanoke darter abundance was most strongly linked to factors that promote larval-juvenile survival. Although similar results might have been obtained by an intensive study of larval or juvenile microhabitat preference, the sampling effort associated with early life history studies is often prohibitive. As demonstrated in Chapter 2, focusing only on adult Roanoke darter microhabitat preference would have failed to demonstrate the importance of larval and/or juvenile rearing habitat. Therefore, identifying potentially influential habitat characteristics was dependent on my ability to jointly discount the importance of adult habitat requirements and highlight the importance of habitat types that promote survival of early life-stages. I could not have achieved this by sampling at a single spatial scale.

For logperch, there was evidence from both microhabitat and large-scale spatial sampling that adult habitat requirements may be of primary importance in determining the distribution and abundance of this species. Although microhabitat sampling would have identified the importance of riffle/run habitat, it would have failed to identify the influence of adjacent pool habitat. Although I was unable to determine the relative importance of pool and riffle habitats in the population dynamics of the Roanoke logperch, information obtained by sampling at multiple scales will allow future researchers to focus on the functional significance of these two disparate habitat

configurations to logperch survival. Again, sampling at a single spatial scale would not have allowed me to identify these relationships.

There was little evidence that a single habitat type, spatial scale, or life stage was of primary importance to the black jumprock. Southwood (1977) suggested that the ability of populations to persist depends on the spatial and temporal constancy and predictability of the resources required by that population and that organisms "sample" habitat at varying spatial and temporal scales. One potentially useful strategy when required resources are unpredictably patchy, is to increase the spatial area sampled by increasing mobility. As I argued earlier, the jumprock is the most vagile of the three study species. If this vagility is an adaptive response to spatial variability in some required resource, then even my largest spatial scale may not have been sufficient to identify the habitat characteristics important to this species. Successful application of habitat models to highly mobile forms will therefore depend on specification of the area of stream used during the course of their life and sampling of habitat use and availability at that scale.

In summary, the multiple-scale sampling failed to produce management level habitat models due to my inability to identify the functional significance of types of habitat used by the three study species. Although habitat preference was demonstrated, the preferred habitat was not necessarily the resource limiting population abundance. Despite this failure, the approach succeeded in identifying potentially important habitat types and life stages for two of the three species. Therefore, multiple-scale sampling shows promise as an initial reconnaissance technique where limited prior information exists about resource limiting a species' distribution and abundance.

Literature Cited

- Addicott, J. F., J. M. Aho, M. F. Antolin, D. K. Padilla, J. S. Richardson, and D. A. Soluk. 1987. Ecological neighborhoods: scaling environmental patterns. *Oikos* 49:340-346.
- Anderson, R. M., and R. B. Nehring. 1985. Impacts of stream discharge on trout rearing habitat and trout recruitment in the South Platte River, Colorado. Pp. 59-64 *in* Olson, F. W., R. G. White, and R. H. Hamre, (eds.) Symposium on small hydropower and fisheries. American Fisheries Society. Bethesda, MD.
- Angermeier, P. L. 1987. Spatiotemporal variation in habitat selection by fishes in small Illinois streams. Pp. 52-60 *in* Matthews, W. J. and D. C. Heins (eds.). Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press. Norman.
- _____. 1992. Predation by rock bass on other stream fishes: experimental effects of depth and cover. *Environmental Biology of Fishes* 34:171-180.
- Austen, D. J., P. B. Bayley, and B. W. Menzel. 1994. Importance of the guild concept to fisheries research and management. *Fisheries* (Bethesda) 19(6):12-20.
- Bain, M. B. and J. T. Finn. 1991. Analysis of microhabitat use by fish: investigator effect and investigator bias. *Rivers* 2:57-65.
- _____ and J. M. Boltz. 1989. Regulated streamflow and warmwater stream fish: a general hypothesis and research agenda. U.S. Department of the Interior Biological Report 89(18). 28p.
- Balon, E. K. 1975. Reproductive guilds of fishes: a proposal and definition. *Journal of the Fisheries Research Board of Canada* 32:821-864.
- Barret, P. J. and O. E. Maughan. 1994. Habitat preferences of introduced smallmouth bass in a central Arizona stream. *North American Journal of Fisheries Management* 14:112-118.
- Benke, A. C. 1990. A perspective on America's vanishing streams. *Journal of the North American Benthological Society* 9:77-88.

- Bergstedt, R. A. and D. R. Anderson. 1990. Evaluation of line transect sampling based on remotely sensed data from underwater video. *Transactions of the American Fisheries Society* 119:86-91.
- Berkman, H. E. and C. F. Rabeni. 1987. Effect of siltation on stream fish communities. *Environmental Biology of Fishes* 18:285-294.
- Beverton, R. H. and S. J. Holt. 1957. On the dynamics of exploited fish populations. *Fishery Investigations, Series II, Marine Fisheries, Great Britain Ministry of Agriculture, Fisheries and Food* 19.
- Binns, N. A. and F. M. Eiserman. 1979. Quantification of fluvial trout habitat in Wyoming. *Transactions of the American Fisheries Society* 108:215-228.
- 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.
- Brown, K. L. 1986. Population demographic and genetic structure of plains killifish from the Kansas and Arkansas River basins in Kansas. *Transactions of the American Fisheries Society* 115:568-576.
- Brown, L. and J. F. Downhower. 1982. Summer movements of mottled sculpin, *Cottus bairdi*, (Pisces: Cottidae). *Copeia* 1982:450-453.
- Brussock, P. P., A. V. Brown, and J. C. Dixon. 1985. Channel form and stream ecosystem models. *Water Resources Bulletin* 21:859-866.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance sampling: estimating abundance of biological populations. Chapman and Hall, London. 446 p.
- 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 Wilmington District. U. S. Army Corps of Engineers. Wilmington, NC. 115 Pp.

- Burkhead, N. M. and R. E. Jenkins. 1991. Fishes. Pp. 321-409 in K. A. Terwilliger, ed. Virginia's endangered species. McDonald and Woodward, Blacksburg, Virginia.
- Burnham, K. D., D. A. Anderson, and J. L. Laake. 1980. Estimation of the density of animals from line transect sampling of biological populations. Wildlife Monographs 72. 202 p.
- Capone, T. A. and J. A. Kushlan. 1991. Fish community structure in dry-season stream pools. Ecology 72:983-992.
- Cheslak, E. F. and J. C. Garcia. 1988. An analysis of the effects of various smoothing and curve-fitting techniques on the accuracy of suitability functions. Pp. 259-283 in Bovee, K. and J. R. Zuboy, (eds.) Proceedings of a workshop on development and evaluation of habitat suitability criteria. U. S. Fish and Wildlife Service, Biological Report 88(11). Washington, D. C.
- Chutter, F. M. 1969. The effects of silt and sand on the invertebrate fauna of streams and rivers. Hydrobiologia 34:57-76.
- Connell, J. H. and W. P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. American Naturalist 121:789-824.
- Crain, B. R., K. P. Burnham, D. R. Anderson, and J. L. Laake. 1979. Nonparametric estimation of population density for line transect sampling using Fourier series. Biometrical Journal 21:731-748.
- Dolloff, C. A. and G. H. Reeves. 1990. Microhabitat partitioning among stream-dwelling juvenile coho salmon, Oncorhynchus kisutch, and Dolly Varden, Salvelinus malma. Canadian Journal of Fisheries and Aquatic Sciences 47:2297-2306.
- van Dorp, D. and P. F. M. Opdam. 1987. Effects of patch size, isolation and regional abundance on forest bird communities. Landscape Ecology 1:59-73.
- Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65:169-175.
- Eberhardt, L. L. 1968. A preliminary appraisal of line transects. Journal of Wildlife Management 32:82-88.

- _____. 1978. Transect methods for population studies. *Journal of Wildlife Management* 42:1-31.
- Emlen, J. T. 1971. Population densities of birds derived from transect counts. *Auk* 88:323-342.
- Ensign, W. E., K. N. Leftwich, P. L. Angermeier, and C. A. Dolloff. *in press*. Factors influencing fish recolonization following a large-scale stream disturbance. *Transactions of the American Fisheries Society*.
- Etnier, D. A. and W. C. Starnes. 1993. *The fishes of Tennessee*. University of Tennessee Press, Knoxville, Tennessee. 681 pp.
- Evans, J. W. and R. L. Noble. 1979. The longitudinal distribution of fishes in an east Texas stream. *American Midland Naturalist* 101:333-343.
- Fahrig, L. and G. Merriam. 1985. Habitat connectivity and population survival. *Ecology* 66:1762-1768.
- Fahrig, L. and J. Paloheimo. 1988. Effect of spatial arrangement of habitat patches on local population size. *Ecology* 69:468-475.
- Fausch, K. D. and R. J. White. 1981. Competition between brook and brown trout for positions in a Michigan stream. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1220-1227.
- Fausch, K. D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Canadian Journal of Zoology* 62:441-451.
- _____, C. L. Hawkes, and M. G. Parsons. 1988. Models that predict standing crop of stream fish from habitat variables: 1950-1985. General Technical Report PNW-GTR-213, U. S. Department of Agriculture, Forest Service, Portland, OR. 52 pp.
- Ferguson, M. T., S. A. Bruenderman, and P. S. Lookabaugh. 1994. A survey of the Roanoke logperch (*Percina rex*) in the North Fork Roanoke River. Final Report. Virginia Department of Game and Inland Fisheries. Fisheries Division. Blacksburg, VA. 61 pp.
- Flather, C. H. and T. W. Hoekstra. 1985. Evaluating population-habitat models using ecological theory. *Wildlife Society Bulletin* 13:121-130.

- Floyd, K. B., R. D. Hoytt, and S. Timbrook. 1984. Chronology of appearance and habitat partitioning by larval stream fishes. *Transactions of the American Fisheries Society* 113:217-223.
- Fraser, D. F. 1983. An experimental investigation of refuging behaviour in a minnow. *Canadian Journal of Zoology* 61:666-672.
- _____ and R. D. Cerri. 1982. Experimental evaluation of predator-prey relationships in a patchy environment: consequences for habitat-use patterns in minnows. *Ecology* 63:307-313.
- _____, D. A. DiMattia, and J. D. Duncan. 1987. Living among predators: the response of a stream minnow to the hazard of predation. Pp. 121-127 in Matthews, W. J. and D. C. Heins (ed.). *Community and evolutionary ecology of North American stream fishes*. University of Oklahoma Press. Norman.
- Forney, K. A. and M. E. Gilpin. 1989. Spatial structure and population extinction: a study with *Drosophila* flies. *Conservation Biology* 3:45-51.
- Freeman, B. J. and M. C. Freeman. 1994. Habitat use by and endangered riverine fish and implications for species protection. *Ecology of Freshwater Fish* 3:49-58.
- Freeman, M. C. and G. D. Grossman. 1993. Effects of habitat availability on dispersion of a stream cyprinid. *Environmental Biology of Fishes* 37:121-130.
- Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management* 10:199-214.
- Funk, J. L. 1957. Movement of stream fishes in Missouri. *Transactions of the American Fisheries Society* 85:39-57.
- Gerking, S. D. 1959. The restricted movement of fish populations. *Biological Review* 34:221-242.
- Goodman, D. 1987. The demography of chance extinction. Pp. 11-34 in M. E. Soule, ed. *Viable populations*. Cambridge University Press. Cambridge, England.

- Gore, J. A. and J. M. Nestler. 1988. Instream flow studies in perspective. *Regulated Rivers: Research and Management* 2:93-101.
- Gorman, O. T. and J. R. Karr. 1978. Habitat structure and stream fish communities. *Ecology* 59: 507-515.
- Greenberg, L. A. 1988. Interactive segregation between the stream fishes Etheostoma simoterum and E. rufilineatum. *Oikos* 51:193-202.
- _____. 1991. Habitat use and feeding behavior of thirteen species of benthic stream fishes. *Environmental Biology of Fishes* 31:389-401.
- _____ and R. A. Stiles. 1993. A descriptive and experimental study of microhabitat use by young-of-the-year benthic stream fishes. *Ecology of Freshwater Fish* 2:40-49.
- Groshens, T. P. and D. J. Orth. 1994. Transferability of habitat suitability criteria for smallmouth bass, Micropterus dolomieu. *Rivers* 4:194-212.
- Grossman, G. D., A. de Sostoa, M. C. Freeman, and J. Lobon-Cervia. 1987. Microhabitat use in a mediterranean riverine fish assemblage: fishes of the upper Matarrana. *Oecologia* 73: 501-512.
- _____, P. B. Moyle, and J. O. Whitaker, Jr. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. *The American Naturalist* 120:423-454.
- 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 Aquatic Sciences* 45:834-844.
- Harvey, B. C. 1991. Interactions among stream fishes: predator-induced habitat shifts and larval survival. *Oecologia* 87:29-36.
- Heggenes, J. 1988. Physical habitat selection by brown trout (Salmo trutta) in riverine systems. *Nordic Journal of Freshwater Research* 64:74-90.
- Hill, J. and G. D. Grossman. 1987. Home range estimates for three North American stream fishes. *Copeia* 1987:376-380.
- Hill, J. and G. D. Grossman. 1993. An energetic model of microhabitat use for

- rainbow trout and rosyside dace. *Ecology* 74:685-698.
- Hollander, M. and D. A. Wolfe. 1973. *Nonparametric statistical methods*. John Wiley and Sons, Inc. New York. 503 p.
- Horwitz, R. J. 1978. Temporal variability patterns and the distributional patterns of stream fishes. *Ecological Monographs* 48:307-321.
- Jenkins, T. M. Jr. 1969. Social structure, position choice, and microdistribution of two trout species (*Salmo trutta* and *Salmo gairdneri*) resident in mountain streams. *Animal Behaviour Monographs* 2:56-123.
- Jenkins, R. E. and N. M. Burkhead. 1994. *Freshwater fishes of Virginia*. American Fisheries Society, Bethesda, Maryland. 1079 pp.
- Keast, A. and J. Harker. 1977. Strip counts as a means of determining densities and habitat utilization patterns in lake fishes. *Environmental Biology of Fishes* 1:181-188.
- Kessler, R. K. and J. H. Thorp. 1993. Microhabitat segregation of the threatened spotted darter (*Etheostoma maculatum*) and closely related orangefin darter (*E. bellum*). *Canadian Journal of Fisheries and Aquatic Sciences* 50:1084-1091.
- Kinsolving, A. D. and M. B. Bain. 1993. Fish assemblage recovery along a riverine disturbance gradient. *Ecological Applications* 3:531-544.
- Kuehne, R. A. and R. W. Barber. 1983. *The American darters*. University Press of Kentucky. Lexington. 177 pp.
- Kwak, T. J., M. J. Wiley, L. L. Osborne, and R. W. Larimore. 1992. Application of diel feeding chronology to habitat suitability analysis of warmwater stream fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1417-1430.
- Laake, J. L., S. T. Buckland, D. R. Anderson, and K. P. Burnham. 1993. *DISTANCE User's Guide V2.0*. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO. 72 p.
- Layher, W. G. 1983. *Habitat suitability for selected adult fishes in prairie streams*. Doctoral dissertation. Oklahoma State University. 333 pp.

- _____ and K. L. Brunson. 1992. A modification of the Habitat Evaluation Procedure for determining instream flow requirements in warmwater streams. *North American Journal of Fisheries Management* 12:47-54.
- Lambert, T. R. and D. F. Hanson. 1989. Development of habitat suitability criteria for trout in small streams. *Regulated Rivers: Research and Management* 3:291-303.
- Leftwich, K. N. 1994. Habitat models for predicting the occurrence of blotchside logperch (*Percina burtoni*) and tangerine darters (*P. aurantiaca*) in the North Fork Holston River and Little River, Virginia. Master's thesis. Virginia Polytechnic Institute and State University, Blacksburg, Virginia. 103 pp.
- Leonard, P. and D. J. Orth. 1988. Use of habitat guilds of fish to determine instream flow requirements of fish. *North American Journal of Fisheries Management* 8:399-409.
- Lyons, J. 1989. Correspondence between the distribution of fish assemblages in Wisconsin streams and Omernik's ecoregions. *American Midland Naturalist* 122:163-182.
- Mahon, R. 1984. Divergent structure in fish taxocenes of north temperate streams. *Canadian Journal of Fisheries Aquatic Sciences* 41:330-350.
- Mathur, D., W. H. Bason, E. J. Purdy, Jr., and C. A. Silver. 1984. A critique of the instream flow incremental methodology. *Canadian Journal of Fisheries and Aquatic Sciences* 42:825-1094.
- Matthews, W. J. 1986. Fish faunal structure in an Ozark stream: stability, persistence and a catastrophic flood. *Copeia* 1986:388-397.
- _____. 1990. Spatial and temporal variation in fishes of riffle habitat: a comparison of analytical approaches for the Roanoke River. *American Midland Naturalist* 124:31-45.
- _____, J. R. Bek, and E. Surat. 1982. Comparative ecology of the darters *Etheostoma podostemone*, *E. flabellare* and *Percina roanoka* in the Upper Roanoke River Drainage, Virginia. *Copeia* 4:805-814.
- _____, and D. C. Heins. 1987. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press. Norman.

- _____ and L. G. Hill. 1979. Influence of physico-chemical factors on habitat selection of red shiners, Notropis lutrensis (Pisces: Cyprinidae). *Copeia* 1979:70-81.
- McClendon, D. 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.
- McIvor, C. C. and W. E. Odum. 1988. Food, predation risk, and microhabitat selection in a marsh fish assemblage. *Ecology* 69:1341-1351.
- Meffe, G. K. and A. L. Sheldon. 1988. The influence of habitat structure on fish assemblage composition in southeastern blackwater streams. *American Midland Naturalist* 120:225-240.
- 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.
- Murphy, D. D., K. E. Freas, and S. B. Weiss. 1990. An environment-metapopulation approach to population viability analysis for a threatened invertebrate. *Conservation Biology* 4:41-51.
- Nehring, R. B. and R. M. Anderson. 1993. Determination of population-limiting critical salmonid habitats in Colorado streams using the physical habitat simulation system. *Rivers* 4:1-19.
- Neitzel, D. A. and C. D. Becker. 1985. Tolerance of eggs, embryos, and alevins of chinook salmon to temperature changes and reduced humidity in dewatered redds. *Transactions of the American Fisheries Society* 114: 267-273.
- Nielsen, L. A. 1993. History of inland fisheries management in North America. Pp. 3-31 in C. C. Kohler and W. A. Hubert, ed. *Inland fisheries management in North America*. American Fisheries Society. Bethesda, MD.
- Newman, R. M. and T. F. Waters. 1989. Differences in brown trout (Salmo trutta) production among contiguous sections of an entire stream. *Canadian Journal of Fisheries and Aquatic Sciences* 46:203-213.

- Northcote, T. G. and D. W. Wilkie. 1963. Underwater census of stream fish populations. *Transactions of the American Fisheries Society* 92:146-151.
- Nuttall, P. M. and E. D. Bielby. 1973. The effects of china clay on stream invertebrates. *Environmental Pollution* 5:77-86.
- O'Neil, J. L. and A. B. Carey. 1986. When habitats fail as predictors. Pp. 207-208 in J. Verner, M. L. Morrison, and C. J. Ralph, (eds.) *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*. University of Wisconsin Press. Madison, WI.
- Orth, D. J. 1987. Ecological considerations in the development and application of instream flow-habitat models. *Regulated Rivers: Research and Management* 1:171-181.
- _____ 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.
- _____ and O. E. Maughan. 1984. Community structure and seasonal changes in standing stocks of fish in a warm-water stream. *The American Midland Naturalist* 112:369-378.
- Ottaway, E. M. and A. Clarke. 1981. A preliminary investigation into the vulnerability of young trout (*Salmo trutta* L.) and Atlantic salmon (*S. salar* L.) to downstream displacement by high water velocities. *Journal of Fish Biology* 19:135-145.
- Page, L. M. 1983. *Handbook of darters*. Tropical Fish Hobbyist Publications. Neptune City, New Jersey. 271 pp.
- Petit, D. R. 1989. Weather-dependent use of habitat patches by wintering woodland birds. *Journal of Field Ornithology* 60:241-247.
- Petty, J. T. 1994. Patch selection by a predatory benthic stream fish: the role of macroinvertebrate distributions. Master's thesis, University of Georgia, Athens, Georgia.
- Platts, W. D., W. F. Megahan, and G. W. Minshall. 1983. Methods for evaluating stream, riparian, and biotic conditions. General Technical Report INT-138. Ogden, UT. U. S. Department of Agriculture, Forest Service, Intermountain

Research Station.

- Poff, N. L. and J. V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1805-1818.
- _____ and J. V. Ward. 1990. Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management* 14:629-645.
- Power, M. E. 1984. Habitat quality and the distribution of algae-grazing catfish in a Panamanian stream. *Journal of Animal Ecology* 53:357-374.
- _____, W. J. Matthews, and A. J. Stewart. 1985. Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. *Ecology* 66:1448-1456.
- _____ and W. J. Matthews. 1983. Algae-grazing minnows, (*Campostoma anomalum*), piscivorous bass (*Micropterus* spp.), and the distribution of attached algae in a small, prairie-margin stream. *Oecologia* 60:328-332.
- _____. 1987. Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size. Pp. 333-251 in Kerfoot, W. C. and A. Sih (ed.) *Predation: Direct and indirect effects on aquatic communities*. University Press of New England. Hanover.
- Prugh, B. J., F. J. Easton, and D. L. Belval. 1990. Water resources data - Virginia - Water Year 1990: Volume 1. Surface water and surface water quality records.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada Bulletin* 191.
- Riley, S. C., K. D. Fausch, and C. Gowan. 1992. Movement of brook trout (*Salvelinus fontinalis*) in four small subalpine streams in northern Colorado. *Ecology of Freshwater Fish* 1:112-122.
- Robinson, G. R., R. D. Holt, M. S. Gaines, S. P. Hamburg, M. L. Johnson, H. S. Fitch, E. A. Martinko. 1992. Diverse and contrasting effects of habitat fragmentation. *Science* 257:524-526.

- Ross, S. T. 1986. Resource partitioning in fish assemblages: a review of field studies. *Copeia* 1986:352-388.
- _____, W. J. Matthews and A. A. Echelle. 1985. Persistence of stream fish assemblages: effects of environmental change. *American Naturalist* 126:24-40.
- _____, J. A. Baker, and K. C. Clark. 1987. Microhabitat partitioning of southeastern stream fishes: temporal and spatial predictability. Pp. 42-51. *in* Matthews, W. J. and D. C. Heins (eds.). *Community and evolutionary ecology of North American stream fishes*. University of Oklahoma Press. Norman.
- Rubin, S. P., T. C. Bjornn, and B. Dennis. 1991. Habitat suitability curves for juvenile chinook salmon and steelhead development using a habitat-oriented sampling approach. *Rivers* 2:12-29.
- Sabo, M. J. 1993. Microhabitat use and its effect on growth of Age-0 smallmouth bass in the North Anna River, Virginia. Doctoral Dissertation, Virginia Polytechnic Institute and State University, Blacksburg, VA. 174 pp.
- Sale, P. F. and W. A. Douglas. 1981. Precision and accuracy of visual census techniques for fish assemblages on coral patch reefs. *Environmental Biology of Fishes* 6:333-339.
- Salwasser, H. 1986. Modeling habitat relationships of terrestrial vertebrates - the manager's viewpoint. pp. 419-424 *in* J. Verner, M. L. Morrison, and C. J. Ralph, (eds.) *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*. University of Wisconsin Press. Madison, WI.
- Schill, D. J. and J. S. Griffith. 1984. Use of underwater observation to estimate cutthroat trout abundance in the Yellowstone River. *North American Journal of Fisheries Management* 4:479-487.
- Schlosser, I. J. 1987. The role of predation in age- and size-related habitat use by stream fishes. *Ecology* 66:651-659.
- _____. 1990. Environmental variation, life history attributes, and community structure in stream fishes: implications for environmental management and assessment. *Environmental Management* 14:621-628.

- _____. 1991. Stream fish ecology: a landscape perspective. *BioScience* 41:704-712.
- Scott, D. and C. S. Shirvell. 1987. A critique of the instream flow incremental methodology and observations on flow determination in New Zealand. *Proceedings of the Third International Symposium on Regulated Streams*. Pp 27-43.
- Seber, G. A. F. 1982. *The estimation of animal abundance and related parameters*. Hafner Press, New York. 654 p.
- Sheldon, A. 1968. Species diversity and longitudinal succession in stream fishes. *Ecology* 49:193-198.
- Shirvell, C. S. 1989. Habitat models and their predictive capability to infer habitat effects on stock size. Pp. 173-179 in C. D. Levings, L. B. Holtby, and M. A. Henderson (eds.) *Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks*. Canadian Special Publication in Fisheries and Aquatic Sciences 105.
- _____. 1990. Role of instream rootwads as juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) cover habitat under varying streamflow conditions. *Canadian Journal of Fisheries and Aquatic Sciences* 47:852-861.
- _____ and R. G. Dungey. 1983. Microhabitats chosen by brown trout for feeding and spawning in rivers. *Transactions of the American Fisheries Society* 112:355-367.
- Shuler, S. W. and R. B. Nehring. 1994. Using the physical habitat simulation model to evaluate a stream habitat enhancement project. *Rivers* 4:175-193.
- Slaney, P. A. and A. D. Martin. 1987. Accuracy of underwater census of trout populations in a large stream in British Columbia. *North American Journal of Fisheries Management* 7:117-122.
- Slauson, W. L. 1988. Constructing suitability curves from data. Bovee, K. and J. R. Zuboy, (eds.) *Proceedings of a workshop on the development and evaluation of habitat suitability criteria*. U.S. Fish and Wildlife Service Biological Report 88(11). 407 pp.

- Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? *Journal of Animal Ecology* 46:337-365.
- Stalnaker, C. W., B. L. Lamb, J. Hendrikson, K. Bovee, and J. Bartholow. 1995. The instream flow incremental methodology: a primer for IFIM. National Biological Service. Biological Report 29. Washington, D. C.
- Swenson, J. E. 1993. The importance of alder to hazel grouse in Fennoscandian boreal forest - evidence from four levels of scale. *Ecography* 16:37-46.
- Taylor, C. M., M. R. Winston, and W. J. Matthews. 1993. Fish species-environment relationships and abundance relationships in a Great Plains river system. *Ecography* 16:16-23.
- Thomas, D. L. 1970. An ecological study of four darters of the genus Percina (Percidae) in the Kaskaskia River, Illinois. Illinois Natural History Survey Biological Notes 70. 18 pp.
- Tilman, D. 1982. Resource competition and community structure. Monographs in Population Biology 17. Princeton University Press. Princeton, NJ.
- Thresher, R. E. and J. S. Gunn. 1986. Comparative analysis of visual census techniques for highly mobile, reef-associated piscivores (Carangidae). *Environmental Biology of Fishes* 17:93-116.
- Travnichek, V. H. and M. J. Maceina. 1994. Comparison of flow regulation effects on fish assemblages in shallow and deep water habitats in the Tallapoosa River, Alabama. *Journal of Freshwater Ecology* 9:207-216.
- Turner, L. J. and W. C. Mackay. 1985. Use of visual census for estimating population size in northern pike (Esox lucius). *Canadian Journal of Fisheries and Aquatic Science* 42:1835-1840.
- U. S. Fish and Wildlife Service. 1980. Habitat as a basis for environmental assessment. Ecological Services Manual 101. U.S. Department of the Interior. Washington, D. C.
- Vadas, R. L. Jr. 1994. Habitat tools for assessing instream-flow needs for fishes in the upper Roanoke River, Virginia. Doctoral dissertation. Virginia Polytechnic Institute and State University. Blacksburg, VA. 346 pp.

- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893-901.
- _____ and J. A. Wiens. 1991. Forest bird habitat suitability models and the development of general habitat models. U. S. Fish and Wildlife Service, Fish and Wildlife Research 8. 31 pp.
- Vanapeldoorn, R. C., W. T. Oostenbrink, A. Vanwinden, and F. F. Vanderzee. 1992. Effects of habitat fragmentation on the bank vole, Clethrionomys glareolus, in an agricultural landscape. *Oikos* 65:265-274.
- Voos, K. A. and W. S. Lifton. 1988. Development of a bivariate depth and velocity suitability function for Dolly Varden (Salvelinus malma) juveniles. Pp. 307-319 in Bovee, K. and J. R. Zuboy, (eds.) Proceedings of a workshop on the development and evaluation of habitat suitability criteria. USFWS Biology Report 88(11). 407 pp.
- Warren, M. L. Jr., B. M. Burr, D. A. Etnier, and W. C. Starnes. 1991. Fishes of Kentucky and Tennessee: a hierarchical classification of drainages. *Journal of the Tennessee Academy of Sciences* 66:135-140.
- Weiss, S. B., D. D. Murphy, and R. R. White. 1988. Sun, slope, and butterflies: topographic determinants of habitat quality for Euphydryas editha. *Ecology* 69:1486-1496.
- Werner, E. E. J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effect of predation risk on habitat use in fish. *Ecology* 64:1540-1548.
- Wilbur, H. M. 1980. Complex life cycles. *Annual Review of Ecology and Systematics* 11:67-93.
- Whiteside, B. G. and R. McNatt. 1972. Fish species diversity in relation to stream order and physicochemical conditions in the Plum Creek drainage basin. *American Midland Naturalist* 88:90-101.
- Whittier, T. R., R. M. Hughes, and D. P. Larsen. 1988. The correspondence between ecoregions and spatial patterns in stream ecosystems in Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1264-1278.
- Wiens, J. A. 1976. Population responses to patchy environments. *Annual Review*

of Ecology and Systematics 7:81-120.

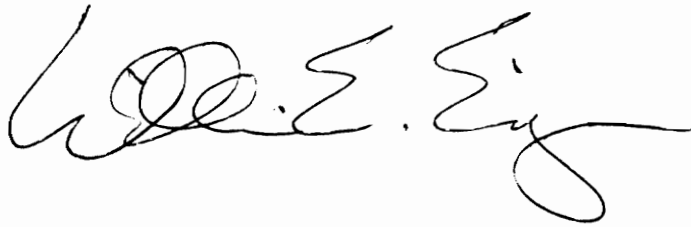
Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.

Wiley, M. T. and C. Tsai. 1983. The relative efficiencies of electrofishing vs. seines in piedmont streams of Maryland. *North American Journal of Fisheries Management* 3:243-253.

Winemiller, K. O. and K. A. Rose. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* 49:2196-2218.

Vita

William Edward Ensign was born on February 20, 1959 in Knoxville, Tennessee. He immediately moved to Chattanooga where he spent the next 18 years of his life. In 1977, he graduated from Brainerd High School. Following a false start at Wake Forest University, he enrolled at George Washington University in 1979, receiving his Bachelor of Arts in Zoology in 1982. A short stint as a research assistant in Washington, D. C. law libraries fostered a love for cold and slimy organisms, so he pursued graduate studies on stream fish at the University of Tennessee, focusing on competition between brook and rainbow trout. He received his Master of Science degree in Ecology in 1988 and subsequently enrolled as a doctoral candidate at Virginia Polytechnic Institute and State University. In August 1995, he became an instructor and research associate in the Department of Fisheries and Wildlife Science at Virginia Tech.

A handwritten signature in black ink, appearing to read "W. E. Ensign". The signature is fluid and cursive, with a large initial "W" and a long, sweeping tail on the "y" of "Ensign".