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EVALUATING STREAM HABITAT IN NORTHERN MICHIGAN:
IMPLICATIONS FOR CONSERVING ARCTIC GRAYLING
(*THYMALLUS ARCTICUS*)

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EVALUATING STREAM HABITAT IN NORTHERN MICHIGAN: IMPLICATIONS FOR CONSERVING ARCTIC GRAYLING (*THYMALLUS ARCTICUS*)

By

Ralph W. Tingley III

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ABSTRACT

EVALUATING STREAM HABITAT IN NORTHERN MICHIGAN: IMPLICATIONS FOR CONSERVING ARCTIC GRAYLING (*THYMALLUS ARCTICUS)*

By

Ralph W. Tingley III

The Arctic grayling was the dominant salmonid species in Michigan's Lower Peninsula but was extirpated from the state in 1936 for reasons theorized to include overfishing, competition with other salmonids, and habitat degradation. Several unsuccessful reintroductions have been attempted, but locations selected for reintroductions were based on remoteness, lack of competitors, and ability to support other trout species, not on habitat characteristics specific to grayling. The goal of this thesis is to consider relationships between landscape predictors and stream habitat and use this information to identify streams that could support grayling. I conducted a literature review to identify historical and current information describing habitat requirements of Arctic grayling. I then examined landscape relationships to in-stream habitat using various multivariate analytical techniques to assess which landscape conditions may control habitat in my study region. I then developed an assessment tool to rate habitat at multiple spatial scales, incorporating predicted landscape effects on habitat and modeled reach data. The Little Manistee, Pine, White, Pere Marquette, Sturgeon, and Sucker Rivers were the highest rated stream segments, and critical in-stream habitat characteristics specific to Arctic grayling were present in these segments. I believe that suitable habitat for Arctic grayling remains within Michigan that can potentially be considered for the expansion of the range restricted Montana subpopulation, though biological limitations may exist. I also believe that my approach can be applied to help restore species in other regions.

To my family and friends.

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TABLE OF CONTENTS

LIST OF TABLES viii

LIST OF FIGURES x

INTRODUCTION 1
Literature Cited 4

CHAPTER 1
ARCTIC GRAYLING (*THYMALLYS ARCTICUS*): HISTORICAL AND NEW PERSPECTIVES FROM ACROSS NORTH AMERICA WITH IMPLICATIONS FOR MANAGEMENT IN MICHIGAN.
Introduction 5
The Arctic grayling
Classification 6
Historical and current range 7
Morphology 8
Habitat requirements 9
Diet and feeding 12
Migration 13
Spawning 16
The decline of the Arctic grayling in Michigan 16
Overexploitation 17
Interspecific competition 18
Habitat loss and degradation 19
Previous recovery efforts in Michigan 21
Montana recovery efforts: past and present 23
Canadian recovery efforts 24
United States legal status 25
Research needs 27
Literature Cited 35

CHAPTER 2
EFFECTS OF MULTIPLE SCALES OF LAND COVER ON NORTHERN MICHIGAN STREAM HABITAT: IMPLICATIONS FOR UNDERSTANDING CONTROLS ON STREAM SYSTEMS.
Introduction 41
Methods
Study area 45
Stream habitat data and collection summary 46
Landscape data 47
Data analysis 48
Results

Landscape and in-stream habitat conditions....53
Patterns of in-stream habitat conditions....54
Relationships between landscape and habitat variables....55
The CSA model....56
CSA results....57
Effects of landscape on flow stability....57
Effects of landscape variables on in-stream habitat....58
Discussion
Overview....60
Physical landscape controls on stream habitat....61
General effects of land cover at different spatial scale: watershed versus riparian zone....63
Specific effects of network and local riparian wetlands on habitat....65
Utility of CSA and RDA....67
Implications....68
Literature Cited....86

CHAPTER 3
DEVELOPMENT AND APPLICATION OF A RATING SYSTEM TO IDENTIFY AND EVALUATE POTENTIAL ARCTIC GRAYLING (*THYMALLUS ARCTICUS*) HABITAT IN MICHIGAN STREAMS
Introduction....91
Methods
Study area....95
Habitat data collection and summary....96
Landscape and modeled reach data....97
Fish data and index of biotic integrity....99
Overview of the assessment tool....99
Scoring stream reaches....101
Rating stream segments....102
Identification of in-stream habitat and validation of assessment tool....103
Results
Landscape conditions....104
Break points of variables included in the habitat scoring system....105
Scored stream reaches....109
Rated stream segments....109
Evaluation of grouped stream segments....110
Identification of in-stream habitat critical to Arctic grayling life history characteristics....111
Presence/absence of other species....112
Discussion
Overview....113
Habitat assessment....114
High rated stream reaches versus former reintroduction locations....116
In-stream habitat of high rated segments....117
Consideration of biological factors....119

The use of thresholds 120
Regional separation 121
Management Implications and Future Needs
Conservation of the Arctic grayling 121
The assessment method 123
Literature Cited 160

APPENDICES
APPENDIX A: Correlations among landscape variables 168

LIST OF TABLES

Table 1.1. Locations, age, and number stocked during most recent Arctic grayling reintroduction attempt (modified from Nuhfer 1992). Streams marked with an asterisk were known to contain the species historically 30

Table 2.1. Mean, range and standard deviation of habitat variables used in analyses 72

Table 2.2. Mean, range and standard deviation of landscape variables used in analyses 73

Table 2.3. PCA results of 22 habitat variables. Four axes explained 65.05% of the variation in habitat data. Bold values indicate variable weights with an absolute value greater than 0.6 that were used to interpret individual axes 74

Table 2.4. Pearson pairwise correlations for landscape variables used in CSA. Variables with correlations higher than an absolute value of 0.2 are shown in bold and were included in the model 75

Table 2.5. Fit statistics for CSA models predicting habitat variables from landscape factors. Statistics include Chi-square goodness of fit (X^2), root mean square error of approximation (RMSEA), Tucker-Lewis Index (TLI) and Normed Fit Index (NFI). Fit of each model is indicated by "yes" or "no." 76

Table 2.6. Standardized total effects generated through CSA of landscape factors on 10/90 flow ratio. Significant effects are shown in bold ($P<0.05$) 77

Table 2.7. Standardized total effects generated through CSA of landscape variables on individual habitat variables. Effects that are statistically significant ($P<0.05$) are shown in bold 78

Table 2.8. Standardized direct effects of landscape variables generated through CSA on individual habitat variables. Effects that are statistically significant ($P<0.05$) are shown in bold 80

Table 3.1. Scores applied to each stream reach over all five filters. Two indicates suitable, 1 is marginal, while 0 is considered unsuitable for Arctic grayling 126

Table 3.2. Variables included in the stream segment rating tool. The reason for including each variable is described briefly, and the sources of data and literature used to create suitability scorings are listed 127

Table 3.3. Length of connected stream segments and the re-ranked score given based on individual reach habitat score 128

Table 3.4. Mean, range and standard deviation (SD) of variables used as filters in the assessment tool throughout the study region 129

Table 3.5. Final rating of a selection of stream segments including top ranked segments, segments where reintroductions were performed, and a collection of other segments where stream field data were available. River segments marked with * are those that historically contained Arctic grayling and a voucher specimen. Those marked with ** are streams where a historical record or written account of Arctic grayling occurs but a voucher specimen does not exist 130

Table 3.6. Percent of geomorphic units averaged across sites in top-ranked stream segments 131

Table 3.7. Riffle substrate composition and embeddedness averaged over all riffles within each high rated stream segment 132

Table 3.8. Mean and maximum depth, average bank stability, average in stream cover and overhanging vegetation for all pools in high rated stream segments 133

Table 3.9. Mean and maximum depth, average bank stability, and average in-stream cover for all runs in high rated stream segments. The average percent of left and right transect points (stream margins) in which silt was the dominate substrate type is also presented 134

Table 3.10. Presence of fish species that could act as competitors or predators of the Arctic grayling within high rated stream segments. Those species marked with as "X" were present in sampling efforts. Fish assemblage data were obtained from the Michigan Department of Natural Resources (DNR) Fish Collection System and Michigan River Inventory databases (Seelbach and Wiley, 1997) 135

Table A.1. Correlations among landscape variables 168

LIST OF FIGURES

Figure 1.1. Historical ranges of the three major Arctic grayling (*Thymallus arcticus*) populations in North America. (Modified from Vincent 1962 and Scott and Crossman 1973) 31

Figure 1.2. Catchments historically inhabited by the Arctic grayling in Michigan. Catchments were based on records from Vincent (1962) and voucher specimen locations from Bailey et al. (2004) 32

Figure 1.3. Shoreline of the Au Sable River after heavy logging in the late 1800's. Much of the riparian zone was cleared, limiting terrestrial input into the stream and eliminating shading. Photo courtesy Lovells Township Historical Society and Glen Eberly 33

Figure 1.4. A log drive on the Au Sable River during the 1800's. Rivers were a useful means of log transportation, however, this had detrimental effects on Michigan streams including loss of riparian zone vegetation, increased sedimentation, increased flashiness, breaks in connectivity, and alteration of substrate composition. Photo courtesy Lovells Township Historical Society and Glen Eberly 34

Figure 2.1. Study sites locations and major river basins in Michigan. Forty five sites were located in the Lower Peninsula and twenty were located in the Upper Peninsula.... 81

Figure 2.2. Model developed for CSA used to evaluate direct effects of landscape factors on stream habitat and indirect effects through stream flow. Error terms are included for endogenous variables and curved arrows linking landscape factors indicate correlations 82

Figure 2.3. Sampling sites plotted over A. the first two axes generated by PCA of habitat variables named "Riffle and coarse substrate" and "Stream stability" respectively and B. The third and fourth axes named "Stream stability" and "Percent pools and overhanging vegetation." Note that two of the axes, responses to flow stability and stream size, show separation of study sites by peninsula 83

Figure 2.4. Percent of total explained variance by RDA predicting habitat variables from groups of landscape variables. A total of 41.2% of the variance within habitat variables was explained by all groups of landscape variables 84

Figure 2.5. Plot of the first two axes from redundancy analysis (RDA) with vectors representing landscape features and points representing physical habitat variables. Gray text represents landscape variables while habitat variables are shown in black 85

Figure 3.1. Major river basins of Michigan historically inhabited by the Arctic grayling (Vincent 1962) with streams from which voucher specimens were collected indicated (Bailey et al. 2006) 136

Figure 3.2. Comparison of modeled July mean temperatures with measured July means for 26 sites in northern Michigan. Modeled temperatures tended to be overestimated for 2009 137

Figure 3.3. Habitat assessment tool used to rate stream segments within Michigan as the most likely to support a population of Arctic grayling. I organized the assessment over 3 scales, the network catchment, network riparian zone, and reach inclusive of 5 filters including drainage area, catchment landscape condition, riparian zone landscape condition, reach condition, and temperature. After the cumulative scoring of a reach, I rescored based on total connectivity and habitat score then rated a stream segment on total length of unsuitable, marginal, and suitable reaches 138

Figure 3.4. Brook trout abundance in stream reaches of my study region plotted against drainage area. As drainage area increases, brook trout abundance decreases, with a marked decrease in numbers occurring at 40 km^2 139

Figure 3.5. 10/90 ratio versus network catchment coarse geology (%) for all reaches in Michigan. Reaches with coarse geology percentages less than 50% generally have 10/90 ratios greater than 8; reaches with coarse geology between 50 and 80% show a decrease in minimum 10/90 ratio values, and those values greater than 80% have a minimum value of about 2. 140

Figure 3.6. Fish Index of Biotic Integrity (IBI) total score versus forest in the network catchment (%) across Michigan. Less than 30% forest is related to increased numbers of sites with low scores. At 30 to 60%, the number of low scores decreases, and few sites with greater than 60% forest have an IBI less than 40 141

Figure 3.7. Fish Index of Biotic Integrity (IBI) total score versus urban land use in the network riparian zone (%) across Michigan. At 6%, sites show marked decrease in IBI score, with few values above 70 present. At 15%, only one value exists above 60 142

Figure 3.8. Fish Index of Biotic Integrity (IBI) total score versus agriculture in the network riparian (%) across Michigan. Sites with agricultural values of 10 to 40% show a decline in IBI score overall, and at 40%, values of agriculture drop sharply 143

Figure 3.9. Visual metric of stream flow stability versus network riparian zone wetlands (%). Sites scored 8 or higher first appear with more than 25% wetlands, and sites with less than 4 do not occur at about 25% wetlands 144

Figure 3.10. Fish Index of Biotic Integrity (IBI) total score plotted against 10/90 flow ratio in Michigan. IBI scores decrease at a 10/90 ratio of 20 145

Figure 3.11. Percent of stream reaches scoring a 0, 1 or 2 at each hierarchical filter. Note that only reach condition and temperature could score a 0. Landscape variables seem to be overall suitable across segments, while drainage area and reach condition (10/90 ratio, 90/50 ratio, and gradient) seem to be the most limiting filters 146

Figure 3.12. Rating of individual stream reaches before application of connectivity. The majority of high ranked reaches occur in the Lower Peninsula, while in the Upper Peninsula the number of high scoring reaches is lower 147

Figure 3.13. Frequency distribution of final stream segment rankings grouped by 0.10 changes in segment score. Black lines indicate breaks between groupings. Sites were grouped by final rating score into top (1.50-1.70), high (1.30-1.49), marginal (1.10-1.29), low (0.90-1.09), and lowest (0.00-0.89). Stream segments with 0.00 values were not included within this figure 148

Figure 3.14. Final rating of stream segments across Michigan. The majority of high rankings streams occurs in the Lower Peninsula 149

Figure 3.15. Descriptive statistics for stream segments grouped by final rating, with statistics for reintroduction sites also shown. Horizontal bars represent mean values, boxes represent the lower and upper quartiles, vertical bars represent the minimum and maximum scores, and asterisks represent outliers. The top ranked group of segments has the highest mean of forest land cover. Reintroduction sites are shown to have a wide range in forest land cover, but the mean falls above 60%, the percentage determined to be suitable for Arctic grayling 150

Figure 3.16. Descriptive statistics for stream segments grouped by final rating, with statistics for reintroduction sites also shown. Horizontal bars represent mean values, boxes represent the lower and upper quartiles, vertical bars represent the minimum and maximum scores, and asterisks represent outliers. All values fall in the suitable range of urban land use (less than 5%) within my study region 151

Figure 3.17. Descriptive statistics for stream segments grouped by final rating, with statistics for reintroduction sites also shown. Horizontal bars represent mean values, boxes represent the lower and upper quartiles, vertical bars represent the minimum and maximum scores, and asterisks represent outliers. Reintroduction sites have the lowest mean agricultural percentage, while the top ranked site have the highest average, yet is below 10%, the break point between good and suitable ranges 152

Figure 3.18. Descriptive statistics for stream segments grouped by final rating, with statistics for reintroduction sites also shown. Horizontal bars represent mean values, boxes represent the lower and upper quartiles, vertical bars represent the minimum and

maximum scores, and asterisks represent outliers. All mean values are above 25%, but low segments have some variation below 25%, while marginal segments has one segment that has less than 25% wetlands present 153

Figure 3.19. Descriptive statistics for stream segments grouped by final rating, with statistics for reintroduction sites also shown. Horizontal bars represent mean values, boxes represent the lower and upper quartiles, vertical bars represent the minimum and maximum scores, and asterisks represent outliers. All mean temperatures fell close to the suitable range of less than 16°C, while lower ranked segments and reintroduction sites have high variance 154

Figure 3.20. Descriptive statistics for stream segments grouped by final rating, with statistics for reintroduction sites also shown. Horizontal bars represent mean values, boxes represent the lower and upper quartiles, vertical bars represent the minimum and maximum scores, and asterisks represent outliers. With increasing coarse geology, average group scores increase. Reintroduction segments have highly variable scores ranging from poor to suitable. Stream segments in the low rated group had high variation in coarse geology as well 155

Figure 3.21. Descriptive statistics for stream segments grouped by final rating, with statistics for reintroduction sites also shown. Horizontal bars represent mean values, boxes represent the lower and upper quartiles, vertical bars represent the minimum and maximum scores, and asterisks represent outliers. Mean values were similar among ranked stream segments, but as rankings decreased groups varied more. Reintroduction sites had a higher mean gradient than what is considered the upper limit for marginal (0.010) with rankings as high as 0.0170 156

Figure 3.22. Descriptive statistics for stream segments grouped by final rating, with statistics for reintroduction sites also shown. Horizontal bars represent mean values, boxes represent the lower and upper quartiles, vertical bars represent the minimum and maximum scores, and asterisks represent outliers. A general trend of decreasing mean values and variance in 10/90 ratio occurs as stream segments increase in rank. Reintroduction sites had a mean 10/90 ratio that was suitable (<10), but had segments that were poor and marginal as well 157

Figure 3.23. Descriptive statistics for stream segments grouped by final rating, with statistics for reintroduction sites also shown. Horizontal bars represent mean values, boxes represent the lower and upper quartiles, vertical bars represent the minimum and maximum scores, while asterisks represent outliers. A general trend of increasing mean values and variance of 90/50 ratio occurs as stream segments increase in rank. Reintroduction sites had a mean 90/50 ratio well below the good score of 55% 158

Figure 3.24. Descriptive statistics for stream segments grouped by final rating, with statistics for reintroduction sites also shown. Horizontal bars represent mean values, boxes represent the lower and upper quartiles, vertical bars represent the minimum and

maximum scores, while asterisks represent outliers. Top and high rated segments have higher mean Procedure 51 total score values than those with below high and reintroduction sites, which all have means close to 100. Cutoff for "good" total Procedure 51 total scores is 105 159

Introduction

Through wide-spread alteration of the landscape, stream habitat has been degraded, changing fish assemblages and causing extinctions as well as reducing the range of many species globally (Helfman 2007). Since 1989, the number of imperiled and extinct freshwater and diadromous fish taxa identified by the American Fisheries Society (AFS) in North America, including distinct populations and seasonal runs, has nearly doubled to 700 (Jelks et al. 2008). Two subpopulations of the Arctic grayling, *Thymallus arcticus,* one extinct and one imperiled, are listed within the conterminous United States.

The Michigan subpopulation of Arctic grayling was extirpated in 1936. Factors theorized to contribute to the loss of the grayling include overfishing and competition from non-native species as well as habitat degradation due to logging and the creation of dams and their subsequent effects on rivers and streams (Vincent 1962). Since this time, several reintroductions have been attempted but none have been successful. The last reintroduction attempts occurred from 1987 to 1991 and were conducted by the Michigan Department of Natural Resources (MDNR). Sites were selected for reintroduction based on remoteness of location, ability to support other trout species including brook trout (*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss)*, and lack of other species, but not based on habitat requirements specific to the Arctic grayling.

The imperiled subpopulation within the upper Missouri River, Montana, may be facing a fate similar to the Arctic grayling in Michigan. Currently, the subpopulation has been restricted to one catchment, the Big Hole River basin, and is thought to occupy approximately 5% of its historic range (Kaya 1992). The decline in abundance is attributed to wide-spread habitat degradation, decreases in flow due to water withdrawals for agriculture, and the expansion of non-native salmonids such as the brown trout, *Salmo trutta,* and the rainbow trout (Kaya 1992). In this region, efforts are underway to save the dwindling subpopulation, and introductions within the state are being attempted to extend its current range. Increased interest in conservation of the Montana subpopulation has led to new research and a greater understanding of the species since the last Michigan reintroductions. Further, it has helped raise the question of whether range expansion to historically occupied northern Michigan would be possible.

With the use of GIS and with new information on habitat characteristics important to Arctic grayling, identifying potentially suitable locations for reintroductions is now possible. Through the landscape approach, we know that landscape factors including vegetative land covers, anthropogenic land uses, and physical characteristics like geology and topography affect physical and biological characteristics of streams (Wang et al. 2003, Allan 2004). If effects on in-stream habitat are understood, landscape conditions can be used as a surrogate or predictor of stream habitat. However, relationships between landscape and in-stream habitat features are complex. Landscape conditions affect the stream in a hierarchical fashion, predicting species assemblages through complex relationships with intermediate mechanisms that alter habitat, such as flow variability (Infante and Allen in press). Between regions, the effects of land cover on habitat and fish assemblage can vary (Utz et al. 2010). The scale at which a landscape variable is summarized also matters, with landscape condition summarized at multiple scales having different effects on stream habitat (Wiens 2002). Once such relationships are better understood, landscape characteristics can be used to help predict where habitat conditions that are specifically needed for a species such as the Arctic grayling may exist within a region, helping to pinpoint locations most suitable for reintroductions and range expansion.

In this thesis, I attempt to identify streams with the highest potential for supporting Arctic grayling habitat within Michigan. I first conduct a literature review of historical information on the species within Michigan as well as new research in other areas. Next, I explore relationships between landscape predictors and in-stream habitat in the potential range for grayling in Michigan to assess how the landscape affects stream habitat in our study region. Finally, I develop an assessment tool capable of identifying streams suitable for Arctic grayling habitat using a hierarchical filter approach encompassing both landscape and modeled reach scale variables.

With this assessment, I intend to answer the question of whether fluvial habitat capable of supporting the Arctic grayling exists in Michigan, while creating a tool that can be applied to any area where landscape data exists. My hope is that the information generated through this research will be useful for conserving a subpopulation of a very unique and imperiled fish species.

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Chapter 1

Introduction

In recent years, concern over the conservation and restoration of native fish species has increased due in part to noted declines in numbers and ranges of many species globally (Helfman 2007). The most recent compilation of imperiled plus extinct freshwater and diadromous fishes in North America clearly supports the need for action, as the list has increased from 363 to 700 taxa since 1989 (Jelks et al 2008). Salmonids represent 11% of listed taxa, with 46% of these being distinct populations or seasonal runs (Jelks et al 2008). Two of the distinct populations included are the fluvial population of *Thymallus arcticus,* the Arctic grayling, found in Montana streams, and the extinct Arctic grayling of Michigan (Jelks et al 2008). With growing concern and attention to the species' decline in both Montana and parts of Canada (Northcote 1993, Clarke et al. 2007, Lamothe and Peterson 2007), potential consideration for the expansion of its range to areas that historically or could potentially support the species may increase.

Because the loss of the Michigan Arctic grayling occurred over 100 years ago in the Lower Peninsula (Mershon 1923), information on life history and habitat characteristics are lacking. However, a historical account of the species' range and decline (Mershon 1923) and a review of historical information relating to its decline as well as its habitat requirements (Vincent 1962) have provided a basis for understanding the species in Michigan. Literature reviews from Alberta (Northcote 1993) and Alaska (Armstrong 1986) as well as information on life history characteristics in British Columbia (Clarke et al. 2007) were extremely useful in identifying sources of information and summarizing habitat needs of the species. New research in the Upper Missouri River, Montana, helped in identifying habitat characteristics suitable for the grayling as well as identifying literature sources (Lamothe and Magee 2003, Lamothe and Magee 2004, Lamothe and Peterson 2007).

The goal of the proceeding literature review is to provide information needed to identify habitat for the Arctic grayling in Michigan, which can then be used for management decisions about possible reintroduction attempts in the future. Objectives include synthesizing information imperative for understanding the extinction of the Arctic grayling in Michigan, to review new research describing habitat characteristics that are important to their survival, to supply the reader with an understanding of previous reintroduction attempts in Michigan, and to describe recovery efforts in other parts of the species' range.

The Arctic Grayling

Classification

The Arctic grayling, *Thymallus arcticus,* is in the subfamily Thymallinae and the family Salmonidae, which include salmon, trout, whitefish, and grayling. *Thymallus* is the lone genus within Thymallinae, with five species existing throughout the world: *T. arcticus, T. thymallus, T. brevirostris, T. grubii* and *T. nigrencens* (Department of Commerce et al. 2008). The name *Thymallus* stems from historical reports describing the odor of the herb "thyme" left on the hands after handling a specimen (McAllister and Crossman 1973). *Arcticus* is the only *Thymallus* species known to exist within North America. *T. thymallus*, the European grayling, is found throughout Europe and parts of Asia. The Arctic grayling and the European grayling are the two most widespread species of the genus. Populations of *T. brevirostris, T. grubii* and *T. nigrenscens* are found in Russia and Mongolia. Due to the disjunct nature of Arctic grayling within North America, several populations were originally considered to be species and later subspecies. The Michigan populations were named *T. tricolor,* those in Montana were named *T. montanus*, and those in Canada, Alaska, and Asia were called *T. signifier* (Vincent 1962). Vernacular names for the Arctic grayling include: grayling, American grayling, bluefish, Back's grayling, sailfin Arctic grayling and Arctic trout (Scott and Crossman 1973). Arctic grayling populations that reproduce in lakes are described as lacustrine populations of the species, and populations within rivers are considered fluvial.

Historical and current range

The Arctic grayling is a holarctic species present in North America and the northeastern portions of Asia (Scott and Crossman 1973). In North America, the species was historically found in three different regions: 1) northwestern Canada and Alaska, extending into Alberta to the south, Nunavut to the east and Alaska to the northwest, 2) Montana, specifically in the upper Missouri River Basin, and 3) the northern two thirds of the Lower Peninsula of Michigan and a one river basin in the Upper Peninsula (Figure 1.1) (Vincent 1962, McAllister and Crossman 1973, Northcote 1993). The two southernmost regions, Montana and Michigan, are considered glacial refuges for the species that occurred following the Pleistocene glaciations (Vincent 1962, Northcote 1993). Within Michigan, the Arctic grayling is believed to have been found in most major rivers in the Lower Peninsula north of and including the White River draining to Lake Michigan in the west, and north of and including the Rifle River draining to Lake Huron in the east. In the Upper Peninsula, records of Arctic grayling occur only in the

Otter and Sturgeon Rivers (Figure 1.2) (Bissel 1890, Vincent 1962). The Arctic grayling has been extinct in Michigan since 1936.

During the 20^{th} century, the range of the Arctic grayling diminished in areas of North America. In northwestern Canada and Alaska, the species remains widespread, yet human-induced alteration of habitat has caused declines in some rivers (Clark et al. 2007). Native fluvial Montana grayling have been reduced in range and now are contained entirely within the Big Hole River system. This decline was attributed to habitat degradation and changes in flow conditions (Kaya 1992, Lamothe and Peterson 2007). Low stream flows due to water withdrawals, diversions for agriculture, and drought are detrimental to Arctic grayling, which depend largely on stable, continuous flow for feeding and migrating to spawning and overwintering habitat (Kaya 1992, Lamothe and Peterson 2007). Introductions are being attempted in several streams, and the species is present in approximately 30 Montana lakes (Rens and Magee 2007). Red Rock Lake and Elk Lake are the only known native lacustrine population of the Arctic grayling in Montana (Campton 2006, Rens and Magee 2007). California, Utah, Wyoming, Colorado, Idaho and Washington support introduced populations of the species in high mountain lakes with limited fishing, with many being supported though heavy stocking (Morrow 1980, McGinnis 1984, Wydoski 2003).

Morphology

The most notable characteristic of the Arctic grayling is its large, sail-like dorsal fin. The fin contains between 17 and 25 rays, while most salmonids have less than 15 (Morrow 1980, Page and Burr 1991). The dorsal fin tends to be larger in males and larger at the posterior end of the fish. The female tends to have the opposite pattern, with the fin higher in the front and lower in the back (McClane 1978). The caudal fin is forked, with the lower lobe extended slightly farther back than the upper. Like all salmonids, grayling have an adipose fin. The body is compressed and slender and is sometimes described as cigar-shaped. Length is approximately 5.5 times its deepest point, which is directly below the dorsal fin (Oosten 1940-41, Page and Burr 1991). Average adult length is about 25 cm in Montana populations while in Alaska and Canada average length is closer to 35 cm (Schrenkeisen 1963, Morrow 1980). In Alaska and Canada, individuals are known to grow larger than those in the southern subpopulations, with fish of over 2 kg taken annually (McClane 1978). The largest known individual was taken from the Katseyedie River in the Northwest Territories, and was 75.9 cm in length and 2.7 kg (McAllister and Crossman 1973, Morrow 1980). Coloration is generally described as grayish purple to olive green on the back, silvery light purple on the sides, and bluish white on the belly. Red, pink, and green spots can appear on the dorsal fin, while darker purple to black spots appear on the body. A long black slash is sometimes notable along the chin (Sigler and Miller 1963). The head is described as moderately small, with a terminal mouth and a large eye (Morrow 1980). In the continental United States maximum age is 10, with most living only to the age of 6 years, while in Canada the oldest individual was 22 years old (DeBruyn and McCart 1974, Wydoski 2003).

Habitat requirements

Arctic grayling prefer intermediate to low gradient streams with a slow, steady flow (Vincent 1962, Kreuger 1981). Adult grayling in Alaska have been recorded spending summer months in areas with a velocity of 0.26 m/s (Kreuger 1981). In Michigan, velocities between 0.30 and 0.61 m/s and a gradient of 0.09-0.28% were considered optimal for summer habitat (Vincent 1962). In Montana, areas with a velocity of 0.21 m/s and a gradient of 0.29% were found to be ideal summer habitat (Liknes and Gould 1981). Overwintering habitat, usually in large pools, had recorded velocities of less than 0.15 m/s in Alaska (Kreuger 1981). In Montana, high grayling densities have been found in pools with overhanging vegetation (Lamothe and Magee 2004). These pools tend to have stable banks, as well as being "high quality pools," a metric defined by maximum depths over two feet, increases in percentage of in-stream cover, and total area (Lamothe and Magee 2004). Arctic grayling in Alaska spawn in fast moving water, usually riffles, with velocities ranging from 0.34 to 1.46 m/s (Kreuger 1981). After hatching, embryos spend three to four days hiding in gravel for cover (Kratt and Smith 1977). Flow stability is important, especially at this life stage, as fry are extremely susceptible to flooding and are easily flushed downstream or out of refuge areas (Nelson 1954). Young of the year move to the side margins of stream channels, with optimal velocities at this time ranging from 0.07 m/s to 0.16 m/s (Elliot 1980). Young of the year in Alberta, the Northwest Territories, and Montana streams have been shown to only use stream margins with little or no silt as nursery areas (Lucko 1992, Barndt and Kaya 2000, Jones et al. 2004).

The Arctic grayling is a cold water species, requiring low temperatures throughout the year. Optimal temperatures for growth and maximum critical temperatures vary depending on the subpopulation studied. In a 1985 study of Arctic grayling in Alaska, estimates of high rates of growth occurred between 7.5 and 16.0 °C (Hubert et al.1985). The lethal temperature for these populations was determined to be 20.0 °C (Hubert et al. 1985), while recent work in Montana identified a lethal temperature of 25.0 °C and a stress temperature of 20.0 °C for juveniles and adults (Lamothe and Peterson 2007). This geographic difference in lethal temperature may be explained by the differences in stream temperature regimes. In Alaska and Canada, the species may be acclimated to lower temperatures throughout the year than those of Montana, lowering both the optimal growth and lethal temperature. For example, in the laboratory, Arctic grayling acclimated at 8.4 °C have a lethal temperature of 23.0 °C, while those acclimated at 16.0 and 20.0 °C had a lethal temperature of about 25.0 °C (Lohr et al. 1996). The latter two acclimation temperatures were used to mimic stream conditions in Montana.

Arctic grayling are not limited by dissolved oxygen (DO) levels to the same extent as other salmonids. In overwintering areas, DO levels have been recorded as low as 0.6 mg/l (Bendock 1980). Modeled optimal DO levels during low flow summer conditions are greater than 4 mg/l, with a critical level of 2 mg/l. An optimal summer DO level is estimated to be 6 mg/l (Hubert et al. 1985). In comparison, brook trout have been shown to have a critical value of 4 mg/l in overwintering conditions and 5 mg/l in summer conditions while optimal DO for summer conditions was estimated to be about 9 mg/l (Raleigh 1982).

Adults are known to inhabit areas within the main flow of the stream, using depth as cover (Byroth and Magee 1998). However, in Alaska, juvenile grayling in both the tributaries and the main channel use large woody debris (LWD) and large boulders for shelter from predators (Kreuger 1981). This suggests that in-stream cover has significant implications for Arctic grayling at early life stages, but may become less important with age.

Substrate composition in streams supporting Arctic grayling varies by region, as well as between spawning, feeding, and overwintering habitat. Grayling streams contain spawning areas characterized by a gravel bottom (Tack 1971, Shepard and Oswald 1989). In Alaska, spawning riffles are dominated by pea-sized gravel (0.08 to 38.10 mm; Tack 1971, Tack 1973). Substrates in British Columbia were composed of 10-20% fine sediment, 30-80% gravel and 10-50% boulder (Butcher et al. 1981). In the Big Hole River, Montana, substrate composition consisted of 20% fine sediments, 50% fine gravel and 30% large gravel (Shepard and Oswald 1989). The U.S. Fish and Wildlife Service (USFWS) habitat suitability model developed for Alaskan Arctic grayling estimated optimal spawning sites as having greater than 20% fine gravel, and less than 10% fine sediments (Hubert et al. 1985). Earlier work by Liknes (1890) estimated that 85% of sites with Arctic grayling in the Big Hole River were either cobble (6.4-26.0 cm) or gravel (2.0-6.3 cm). Although the specific substrate composition of spawning sites for Arctic grayling in Michigan is unknown, rivers that they inhabited tended to be sandy, but had fine gravel present in riffles and bars throughout the stream (Vincent 1962). Spawning in Michigan was not recorded in areas of mud, silt or clay. Eggs found in these substrate types were thought to have drifted and become attached to local vegetation (Nelson 1954, Bishop 1971).

Little is known about effect of pH on Arctic grayling. The USFWS habitat suitability index indicates that grayling occupy streams that have a pH of 6.4 to 7.8 (Hubert et al. 1985). Low pH has been proposed as a contributing factor to the failure of lake introductions in the Upper Peninsula of Michigan (Nuhfer 1992).

Diet and feeding

Grayling begin to feed about four days after hatching (Brown and Buc 1939). Fry feed mostly on zooplankton, and as they proceed through their first year of life, they shift towards a diet consisting of small macroinvertebrates (Jones et al. 2003). Juvenile adults tend to focus mainly on stream drift, including terrestrial and benthic invertebrates (Vascatto 1970). Adults are largely insectivorous, though they also consume small mammals (DeBruyn and McCart 1974), the eggs and fry of other fish species, and sometimes their own eggs (Alt 1980). Although the diet of Arctic grayling varies among regions, it is generally assumed that they are opportunistic and aggressive feeders (Vincent 1962, Hubert et al. 1985, Northcote 1993).

Adult fish hold in upper reaches of the main stem, while juvenile fish are located in the lower reaches (Hughes 1998). It is believed that this occurs because of the favorable conditions upstream, including increased stream drift and lower temperatures (Hughes 1998). In individual pools, larger fish tend to be found on the upstream margins, while smaller ones tend to be on downstream margins (Hughes 1998).

O'Brien et al. (2001) found that Arctic grayling feeding efficiency was unaffected by current velocity in artificial conditions, but a relationship between availability of more stream drift was balanced by a decrease in the species' ability to accurately target prey in higher flow conditions. However, in natural systems, increased turbidity can lead to a decrease in feeding success (McLeay et al. 1987).

Migration

The fluvial Arctic grayling is a migratory species that generally completes its entire life cycle within one or more streams, although historical records in the Midwest indicate that Arctic grayling were caught in Lake Michigan (Vincent 1962). Migrations take place during the spring and fall, allowing the species access to habitats for overwintering, spawning, and summer feeding (Armstrong 1986, Northcote 1993).

Much of the following description of Arctic grayling migration patterns was interpreted from Armstrong (1986) and Northcote (1993), with emphasis on Alaska and British Columbia populations. In these areas, Arctic grayling begin their life in spring spawning areas. This habitat tends to be in tributary streams consisting of fine gravel or the upper reaches of large, unsilted rivers. Age-0 grayling will spend the majority of the spring and fall near the spawning site in backwaters, side channels and stream margins. In the winter months, grayling will migrate to overwintering sites. Occasionally, age-0 grayling will not leave spawning sites, indicating that in some cases these sites can also serve as overwintering habitat for young of year. In colder regions, overwintering locations enable fish to survive when feeding and spawning areas are frozen (Tack 1980, Armstrong 1986). Arctic grayling will remain in these areas until spring, at which time they will travel to a feeding area or a spawning area if they are sexually mature. Spring migrations tend to occur anywhere between mid-April and late July (Tack 1980, Shepard and Oswald 1989, Northcote 1993), and are triggered by increased temperature and flow (Shepard and Oswald 1989). While mature grayling return to spawning sites, juveniles migrate to summer feeding sites. Summer feeding sites are usually large, unsilted rivers with long deep runs and in some cases, clear tributaries. In autumn, the migration cycle resumes, with all grayling returning to overwintering areas. Buzby and Deegan (2000) found that in the Kuparuk River, Alaska, the majority of Arctic grayling return to the same habitat each year.

Arctic grayling sometimes migrate long distances. Lamothe and Magee (2003) found that Arctic grayling in the Big Hole River (Montana) move on average about 40 km annually. Alaskan populations were shown to have migrations up to 100 km, with most fish migrating between 25 and 75 km a year (West et al. 1992). In Michigan, limited connectivity of essential habitat throughout stream reaches was posed as one of the reasons why stream introductions may have failed (Nuhfer 1992), although the historical presence of beaver in the region call to question the ability of the species to migrate long distance (Vincent 1962).

An example of short migration routes due to close proximity of specific habitat is the Sunnyslope Canal population in Teton County, Montana. Sunnyslope is a small irrigation canal that flows from the Pishkun Reservoir. The Arctic grayling has existed within the canal since an introduction in the 1940's (Barndt and Kaya 2000). Grayling exist only in the canal and within 6 km of the reservoir because during the summer, the rest of the 55 km canal goes dry. Arctic grayling overwinter in small residual pools in this upper section and then spawn in small riffles created by release from the dam in spring. Outflow from the reservoir is through releases covered by 2.5 cm grates, therefore limiting the size and age of potential predators from exiting the reservoir and entering the canal (Barndt and Kaya 2000). For the 60 years since its origin, Sunnyslope Canal has supported a self-sustaining population of Arctic grayling. Due to increased interest in protecting the fluvial Arctic grayling within Montana, this population is now monitored and managed (Barndt and Kaya 2000). The lack of connectivity to numerous spawning riffles with the lack of flow to pools during winter months suggest that habitat conditions within the canal would not be conducive to a sustainable population. However, Sunnyslope canal has the conditions of larger river systems that Arctic grayling historically inhabited: low gradient, stable flow, limited predation and competition from invasive species, and shallow gravel spawning areas (Barndt and Kaya 2000).

Spawning

Spawning occurs after spring migrations over riffle areas of fine gravel, usually in upper tributaries or areas of the main channel with higher velocities (Vincent 1962). Unlike most salmonids, grayling do not build nests or redds and instead are broadcast spawners (Tack 1971). Males are territorial, establishing territories about 60 m^2 (Tack 1971). Females remain in surrounding pools or deeper areas, entering male territories only for short periods to spawn (Tack 1971). The dorsal fin plays a role in the mating ritual, as the male will fold it over the back of the female, pressing her slightly into the gravel substrate (Tack 1971). Eggs are then deposited by the female, some being buried, but most adhering to gravel at other points within the riffle. In lakes, spawning can take place in inlets and outlets as well as within the lake itself (Bendock 1980, Armstrong 1986), with young of year potentially holding with streams until moving to lakes to overwinter (DeBruyn and McCart 1974).

The decline of the Arctic grayling in Michigan

The Arctic grayling decline in Michigan was first widely recognized in the 1880's although historical accounts suggest an even earlier period (Vincent 1962). Extirpation of the species from Michigan waters is believed to be related to three main factors: overexploitation, competition with other salmonids, and habitat loss and degradation (Vincent 1962). The background and evidence for a role of these factors is given below.

Overexploitation

Its desirability as a food source coupled with ease of catch made grayling a target to anglers of all skill levels and exploitation of the species was common. Perhaps due to this ease in angling, sport fishing for grayling was extremely popular to the people of Michigan. An unknown author describes his experiences in fishing for the Arctic grayling in the late 1800's:

> "The following day we fished along leisurely until we had our live-boxes, containing each sixty pounds, so full that the fish began to die. Then we passed over splendid pools in which we could see large schools of grayling on the bottom without casting a fly; for we would not destroy them in mere wantonness."
>
> \- From *Michigan Grayling*, Scribers bound magazines, 1879.

Outside the state, the fish gained popularity as well. A small commercial fishery that shipped grayling to the Chicago area was believed to exist in some parts of Michigan (Vincent 1962), while angling for the species made Michigan a popular tourist location in the Midwest (Mershon 1923). While some anglers like those in the previous quote caught only what they intended to keep, the intense waste of a seemingly endless resource by an expanding group of anglers was apparent in the Au Sable River:

> "Yet they are not out of reach of slaughter, for while I was in the river in August last two large camps, all non-residents and strangers killed five thousand fish, not going beyond five miles of the mouth of the North Branch. They salted and carried away at least half of them. Many were eaten, more were wasted. For two miles below from their camps decaying fish whitened the stream, and the offal

and fish entrails left unburied in camp tainted the air, as the dead fish poisoned the water"

- From an 1878 article in *Recollections of My Fifty Years in Hunting and Fishing"*, W.B. Mershon, 1923.

Because of the intense fishing pressure described in the accounts above, overexploitation is believed to have caused initial declines in Arctic grayling populations throughout the Lower Peninsula (Vincent 1962).

Interspecific competition

Exacerbating impacts of overfishing, competition was a second factor that may have contributed to decline and extinction of the Arctic grayling. Historically, the brook trout was known to inhabit streams flowing north while those flowing east and west contained grayling (Mershon 1923). In 1870, brook trout were first stocked into other streams within the Lower Peninsula, and by 1883, all streams that contained grayling also contained brook trout (Mershon 1923). The following description of trends in species abundance was described by Vincent (1962). After their colonization of a stream, brook trout numbers would increase and grayling would decline over the next 20 years. Some believed at the time that predation by the brook trout was the cause of grayling decline (Mershon 1923). As the populations of Arctic grayling diminished in the stream, their individual size increased, and few fry or yearlings were seen. This led to the belief that brook trout and perhaps introduced rainbow trout, *Oncorhynchus mykiss*, were preying on Arctic grayling eggs and fry (Mershon 1923). However, at least three rivers in the Lower Peninsula were known to support both grayling and brook trout before 1850 and before declines were described in the 1870's: the Jordan, Boardman, and the Boyne, suggesting that these species may have coexisted (Unknown 1879, Vincent 1962). Further, in Michigan's Upper Peninsula, the Arctic grayling was only known to inhabit the Otter and Sturgeon Rivers within the Sturgeon River basin on the Keweenaw Peninsula, where brook trout were also present (Vincent 1962).

There is further recent evidence that brook trout and the Arctic grayling can coexist. Brook trout and Arctic grayling occupy different stream microhabitats, and intraspecific competition is expected to be greater than interspecific competition where gradients are low and species coexist (Byroth and Magee 1998). Vincent (1962) notes that although grayling were last recorded in Michigan in the upper tributaries and higher reaches of large streams, they probably were historically more prominent in lower reaches with steadier flow and lower gradient. It is suspected that populations were driven to upper reaches of stream systems in search of suitable habitat as logging and agriculture increased in lower reaches. In these higher gradient areas, the grayling may have been more likely to be outcompeted by species that prefer such conditions, such as the brook trout (Vincent 1962). In summary, the proposed competitive displacement of grayling by brook trout in Michigan does not seem to be supported by current research. While predation and competition by other species of trout is not well documented, it is believed that the presence of brown trout, *Salmo trutta,* and rainbow trout in the Upper Missouri river may have caused the initial restriction of species range in Montana (Kaya 1992, Campton 2006)

Habitat loss and degradation

Intense deforestation of northern Michigan is believed to be a main cause of habitat degradation in streams formerly occupied by Arctic grayling. The removal of

Michigan's white pines (*Pinus strobus)* occurred throughout the mid and late 1800's, but largely between 1875 and 1895 (Maybee 1960, Dickmann and Leefers 2003). This rapid loss of forest was a result of efforts to rebuild Chicago after the Chicago fire of 1871 (October 18) when over 17,500 buildings were destroyed (Dickmann and Leefers 2003).

The streams were the main artery for transport of logs, an open source for logging companies where logs were piled on rollways or cleared riparian areas until spring when they were pushed down river during high seasonal flows (Dickmann and Leefers 2003)(Figure 1.3). Loss of riparian woodland could have caused the decline of terrestrial input of stream drift and the warming of river waters. Large woody debris (LWD) was removed to allow for more efficient transportation of logs downstream (Vincent 1962) (Figure 1.4). The loss of LWD caused both the loss of refuge areas important to juvenile development and a decrease in the abundance of macroinvertebrates and stream drift (U.S. Forest Service 1984, Benke et al. 1985).

Foraging and spawning habitats were greatly altered when logs would scrape banks and bottoms in shallow areas. Stretches of fine gravel riffles once used for spawning could have been covered by fine sediments and sand (Maybee 1960, Vincent 1962, Miller 1966). The disappearance of young of year and fry that were thought to be associated with brook trout and rainbow trout predation may in fact be linked to a loss of spawning habitat induced by logging's large scale alterations (Vincent 1962, Miller 1966). Increased sand and silt could have also reduced interstitial spacing important for macroinvertebrate survival, therefore altering and limiting food supply for all stream species. Not only did the logging affect habitat conditions, but also took a physical toll on individuals. As Miller (1966) describes

> "When the logs came down the rivers they raked the spawning beds, destroyed the eggs or the young fish. In the jam the bark was ground off the Norway pines, filling the water with fine particles that sifted into the graylings gills. I found innumerable dead with festered gills, and in every case the fine particles of bark were the cause."
>
> - From "*The Old Au Sable*" by H. B. Miller 1966

Dams were built and managed by private companies and greatly altered flow regimes in the region (Vincent 1962, Dickman and Leefers 2003).The build-up of water behind these dams as well as their quick release led to bursts of high flows in systems historically know for being stable and slow (Vincent 1962). The dams themselves fragmented connectivity within stream systems, most likely destroying grayling migration routes. Due to the intense and multi-leveled impacts of logging on stream health, it would seem that habitat modification is a likely factor contributing to the local extinction of the Michigan subpopulation.

Previous recovery efforts in Michigan

Between 1906 and 1991, over 3,000,000 grayling were stocked in Michigan waters, with two-thirds of all individuals being stocked between 1926 and 1936 (Nuhfer 1992). Arctic grayling were never successfully re-established in Michigan through these efforts (Leonard 1949, Nuhfer 1992). The most recent stocking attempts occurred from 1987 to 1991 by the Michigan Department of Natural Resources (Nuhfer 1992). Stocking locations were selected based on their ability to support trout species, remoteness of location, and scarcity of other fish species (Nuhfer 1992). Yearlings were stocked from 1987 to 1991 in a total of 13 inland lakes and 7 streams (Table 1.1). Only two of the seven reintroduction streams were known to historically support the species, the Au Sable below Mio Dam and the Upper Manistee (Vincent 1962, Nuhfer 1992). Fry were stocked in East Fish Lake in Montmorency County in 1991 (Nuhfer 1992). Eggs were taken from a Wyoming lake for 1987, 1989, 1990 and 1991 introductions, and this source was presumably a result of previous introductions as there are no historical records of Arctic grayling in Wyoming. The 1988 introduction used eggs from a creek in Canada's Northwest Territories where Arctic grayling are native (Nuhfer 1992).

Although Arctic grayling persisted in some of the stocked Michigan lakes up to 5 years after introductions, no natural reproduction was detected, and this was proposed to result from a lack of movement of grayling to spawning inlets and outlets (Nuhfer 1992). Nuhfer (1992) noted that spawning might have been limited by the absence of imprinting to spawning areas. Overall survival was hypothesized to be limited by competition for food, predation by other species, low pH, hooking mortality, illegal harvest, and fungal infections (Nuhfer 1992). In streams that were stocked with grayling, fish disappeared after six months, and no reproduction was detected (Nuhfer 1992). Stream fish were believed to have immediately traveled downstream after being introduced, taking them into large reservoirs or the Great Lakes, reducing their chance of survival and reproduction. Reasons for failed restoration included poor habitat quality, fragmentation of streams by dams, high water temperatures, overfishing and illegal taking in open fishing areas, and that lacustrine populations were ill adapted to survive in fluvial systems (Nuhfer 1992). Nuhfer (1992) concluded that Michigan did not have the kinds of large, high quality streams with few competing species that grayling require. He noted that future dam removal might lead to increased availability of grayling habitat. This conclusion was based on the inability of Arctic grayling to establish a population in any of the seven rivers where introductions took place.

Montana recovery efforts: past and present

In recent years, increased awareness of the declining Arctic grayling subpopulations in other regions has prompted new approaches to conservation (Northcote 2003, Lamothe and Peterson 2007). In Montana, the last native fluvial population (Big Hole River) experienced a sharp decline in the mid-1980's. This led to the formation of the Arctic Grayling Recovery Program (AGRP), a consortium headed and largely funded by the Montana Fish, Wildlife and Parks. The program contains representatives from the U.S. Fisheries and Wildlife Service (USFWS), the U.S. Forest Service (USFS), the Montana Bureau of Land Management, the Montana Natural Heritage Program, Montana State University, the University of Montana, the National Park Service, the Montana Chapter of the American Fisheries Society, and Montana Trout Unlimited (Rens and Magee 2007). The AGRP's goals are to 1) understand the factors contributing to the decline of the Montana Arctic grayling population, 2) monitor and research current populations, 3) restore habitat, and 4) keep the public informed of all activities and progress (Rens and Magee 2007). Since 1991, reports on current populations of the species, recovery efforts and techniques used, and new research have been issued annually (Rens and Magee 2007).

In 2006, the AGRP developed and implemented a Candidate Conservation Agreement with Assurances (CCAA). This agreement states that any private landowner who voluntarily improves habitat and works to keep the Arctic grayling off the Endangered Species List will not be subject to further restrictions if the species becomes listed (Lamothe and Peterson 2007). Some local ranchers and private landowners have demonstrated support for the project and have restore habitat by enrolling over 73,000 acres by the end of 2006 (Lamothe and Peterson 2007). Techniques such as increasing and stabilizing flows, restoring riparian vegetation, and creating fish ladders have been used. Although existing populations have not had sharp increases, the efforts have been successful in preventing extinction of the subpopulation. Landowners along the Big Hole River reduced divergent flows and malfunctioning headgates which control water flow into a canal, and this led to an increase in flow of over 200 cfs during the spawning season from 2005 to 2006 (Rens and Magee 2007). This improved conditions for spawning, and also improved habitat by flushing fine sediment from the system (Rens and Magee 2007). Severe drought has occurred in Montana in recent years, leading many to believe that the Big Hole River population would have become extinct without these conservation efforts (Rens and Magee 2007).

Along with habitat restoration, reintroductions in several fluvial Montana systems are being attempted as part of the Montana AGRP. Historically, introducing Arctic grayling to fluvial systems in Montana has been unsuccessful (Rens and Magee 2007). However, in 2004 remote site incubators (RSIs) were used to introduce grayling eggs instead of stocking hatchery fish (Rens and Magee 2007). This was in response to success in grayling introductions in Red Rock Lake, where RSIs were used to expose grayling eggs to natural physical conditions before hatching (Kaeding and Boltz 2004). Success in maintaining fluvial populations in the Ruby River has since occurred with the use of RSIs, now the only method of reintroduction used by the Montana AGRP.

Canadian recovery efforts

Arctic grayling in some areas of Canada are declining due to habitat alteration and overfishing (Northcote 1993). In Alberta, it is estimated that the Arctic grayling inhabits only 40 percent of its historical range, and the species is now listed as "sensitive" in this province (Alberta Sustainable Resource Development 2005). As of 2010, the Arctic grayling is considered a high priority candidate for listing by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2010). In British Columbia, the Peace River contained a sustainable population of grayling before construction of the WAC Bennett Dam, creating the Williston Reservoir in 1967 (Clarke et al. 2007). Since then, the Peace River population of grayling has diminished and has been classified as critically imperiled (Northcote 1993, Clarke et al. 2007). This has led to a call for further research and for increased attention to potential impacts from human activities (Northcote 1993). Recently, it was discovered that grayling were no longer entering the main stem of the Peace River (now the Williston Reservoir) and that the populations has become spatially segregated into small subpopulations within tributaries (Clarke et al. 2007). This demonstrates how alteration of natural migration routes and the creation of impoundments, as occurred in Michigan, can negatively impact grayling.

United States legal status

Legal status of the Arctic grayling depends on whether fluvial and lacustrine populations are genetically distinct. Possible listing as a threatened/endangered species for grayling began in 1991, when a petition was filed with USFWS to list the fluvial grayling as an endangered species (Rens and Magee 2007). In 1994, the Montana fluvial grayling was classified as a candidate species and as a Distinct Population Segment (DPS) at varying levels. It was believed that differing ability of lacustrine and fluvial populations to maintain position within the stream current was evidence for genetic diversity (Kaya and Jeanes 1995). Lacustrine grayling would travel downstream, while fluvial grayling would hold their position within the stream channel, even after moderate (1 day) acclimation to conditions (Kaya and Jeanes 1995). In 2004, a petition was filed to emergency list the fluvial grayling due to drought conditions in Montana (Rens and Magee 2007). In order to be listed as a DPS, the fluvial grayling had to be considered discrete from other populations of the species and be significant to the future genetic viability of the species (Campton 2006). To meet these criteria, the species had to either be separated from other populations by geographic barriers or by international borders. For the populations in a region to be considered biologically "significant," they have to inhabit an ecological setting that is unusual or unique for the taxa and show evidence that losing the population would create a significant gap in the species' distribution.

On April 24, 2007, the species was removed as a listing candidate for two reasons (Wilson and Katzenberger 2007). First, there was not enough information to conclude that the fluvial Arctic grayling could be listed simply for its genetic differences from that of lacustrine populations. Findings from previous studies were thought to be a result of life history differences. This conclusion was based on a review of genetic information on the species at that time (Campton 2006). However, while Campton (2006) determined that lacustrine and fluvial populations were not genetically discrete, the Big Hole River drainage population in both lakes and rivers was discrete from the Red Rock and Elk Lakes populations in the upper Red Rock River. Therefore, these two groups met the criteria based on genetic discreteness, but little scientific data existed at the time that would justify significance (Campton 2006). Second, it was determined that the loss of the Montana fluvial Arctic grayling would not leave a significant gap in the range of the species (USFWS 2007). Therefore, the Montana population was no longer considered a DPS and would no longer be eligible for candidacy.

After the 2007 ruling by the USFWS, a coalition of groups and individuals including the Center for Biological Diversity, the Federation of Fly Fishers, the Western Watersheds Project, and some individuals, filed a lawsuit over the loss of candidacy (Backus 2007). In May 2009, the USFWS initiated a voluntary remand of their finding to consider the fluvial and/or adfluvial populations a DPS under federal law (USFWS 2009). A new study of population genetic structure demonstrated that grayling from Wyoming, Saskatchewan, and Montana and surrounding lacustrine Arctic grayling were genetically distinct from Canadian populations (Peterson and Arden 2009). Additionally, it found that the Big Hole River subpopulation was the most diverse from Canadian Arctic grayling (Peterson and Arden 2009). This result may play an important role in the final ruling, to be made in August 2010.

Research needs

Given the declining or unsustainable populations of Arctic grayling in the conterminous United States and some areas of Canada, restoration of the species to its native range should be considered. Recent research in Montana has shown that different stocking methods can enhance success of Arctic grayling introductions. The finding that early acclimation to stream flow conditions is important for holding within the current has shown that stocking of later developmental stages such as fingerlings, yearlings or even fry may be reduce survival and establishment (Rens and Magee 2007).

Degraded habitat contributes to Arctic grayling population declines. Recent recovery efforts in areas where the species still exists have shown some success. For example, introduction attempts in the Ruby River, Montana have shown successful use of RSI to produce Arctic grayling that remain within the stream and potentially have reproduced naturally (Rens and Magee 2007). Although populations in the Big Hole River remain low, it is believed that habitat restorations specific to the Arctic grayling's needs, such as increases in flow and flow stability, have saved the population from extinction during severe droughts (Rens and Magee 2007).

While Arctic grayling may be similar to brook trout in some respects, such as the need for stable flows and cold water temperatures, there are important differences in their habitat requirements. Arctic grayling prefer low to moderate gradient streams, while brook trout prefer higher gradient streams. Brook trout use large woody debris and other structure as cover, while Arctic grayling primarily use depth. Brook trout are known to do best in streams with heavy canopy cover (50 – 75%), while Arctic grayling have been shown to thrive in streams with much less (<5%) (Raleigh 1982, Lamothe and Magee 2004). If Arctic grayling were introduced to higher gradient streams, they would likely move to downstream reservoirs if present where they may be subject to predators and high temperatures. Many of the Michigan streams in which Arctic grayling were introduced have a moderately high to high stream gradient and were within 16 km of a reservoir or Great Lake (Nuhfer 1992). This limited connectivity coupled with no acclimation to stream flow could also be a factor for a species that migrates on average 40 km a year to spawning sites, especially if local stream conditions are not optimal. Grayling, unlike brook trout, can survive at low dissolved oxygen levels, a factor that may make them more apt to thrive in lower gradient, slower streams. Brook trout and Arctic grayling spawn in different areas, with the latter largely favoring fine gravel and broadcast spawning. Brook trout construct redds within the riffle and select spawning locations based on upwellings as opposed to substrate size (Raleigh1982). Arctic grayling seem most suited for large, deep streams with runs and pools that have steady, cold flows and minimum human influence.

Efforts to reintroduce grayling should first attempt to identify those locations most likely to have habitat characteristics that could support the species. Using ArcGIS, I can examine large regions for suitable Arctic grayling habitat using relationships known to exist between landscape and habitat conditions. This would allow for more in-depth analysis of the existence of suitable habitat within the state and help direct managers towards future decisions on possible reintroductions.

Table 1.1: Locations, age, and number stocked during most recent Arctic grayling reintroduction attempt (modified from Nuhfer 1992). Streams marked with an asterisk were known to contain the species historically.

Year	County	Stream/lake	Age	Total stocked
1987				
	Alcona	Horseshoe Lake	yearlings	1500
	Alcona	Reid Lake	yearlings	1500
	Alger	Ackerman Lake	yearlings	1375
	Alger	Chapel Creek	yearlings	800
	Alger	Kettlehole Lake	yearlings	700
	Alger	Section 34 Creek	yearlings	5400
	Alger	Spray Creek	yearlings	5290
	Antrim	Cedar Creek	yearlings	3000
	Crawford	Kneff Lake	yearlings	1424
	Crawford	Manistee River	yearlings	18000
	Grand Traverse	Sand Lake	yearlings	1700
	Houghton	Penegore Lake	yearlings	1000
	Kalkaska	Manistee River*	yearlings	13139
	Luce	Deer Lake	yearlings	1200
	Luce	Sid Lake	yearlings	1000
	Marquette	Mulligan Creek	yearlings	2000
	Montmorency	East Fish Lake	yearlings	1600
	Montmorency	Fuller Pond	yearlings	1500
	Oscoda	Au Sable River*	yearlings	40320
	Schoolcraft	Dutch Fred Lake	yearlings	1000
1988				
	Alger	Ackerman Lake	yearlings	926
	Alger	Section 34 Creek	yearlings	4136
	Alger	Spray Creek	yearlings	4259
	Alcona	O'Brien Lake	yearlings	1334
	Antrim	Cedar River	yearlings	2938
	Crawford	Manistee River*	yearlings	9634
	Luce	Deer Lake	yearlings	840
	Luce	Sid Lake	yearlings	1000
	Oscoda	Au Sable River*	yearlings	13795
1990				
	Alger	Ackerman Lake	4-month fingerlings	1400
	Luce	Deer Lake	4-month fingerlings	900
	Luce	Sid Lake	4-month fingerlings	646
1991				
	Baraga	West Branch Huron	4-month fingerlings	25230
	Luce	Deer Lake	4-month fingerlings	2400
	Luce	Sid Lake	4-month fingerlings	2200
	Marquette	Mulligan Creek	4-month fingerlings	10000
	Montmorency	East Fish Lake	fry	62160

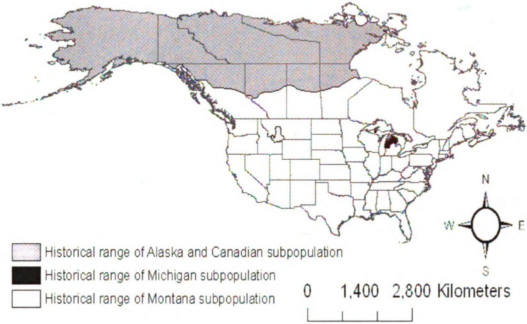

Figure 1.1: Historical ranges of the three major Arctic grayling (*Thymallus arcticus*) populations in North America. (Modified from Vincent 1962 and Scott and Crossman 1973).

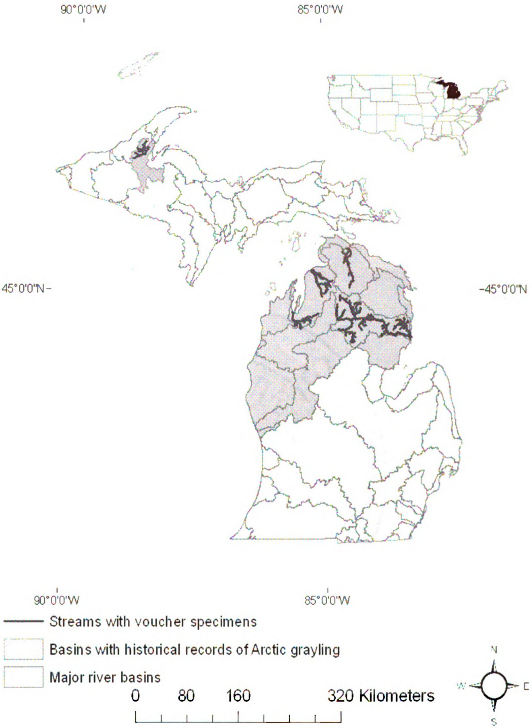

Figure 1.2: Catchments historically inhabited by the Arctic grayling in Michigan. Catchments were based on records from Vincent (1962) and voucher specimen locations from Bailey et al. (2004).

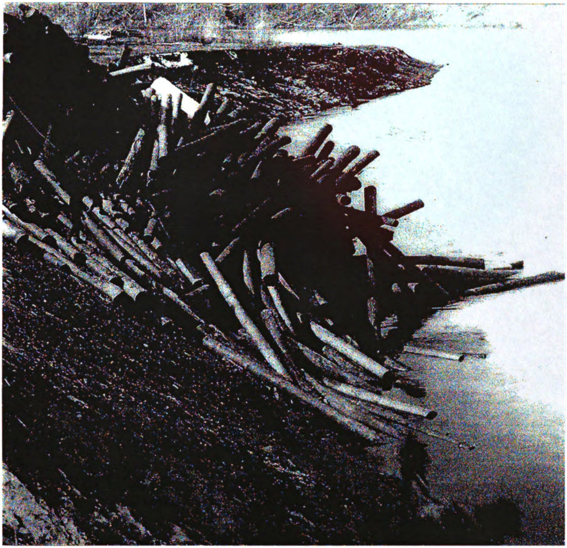

Figure 1.3: Shoreline of the Au Sable River after heavy logging in the late 1800's. Much of the riparian zone was cleared, limiting terrestrial input into the stream and eliminating shading. Photo courtesy Lovells Township Historical Society and Glen Eberly.

Figure 1.4: A log drive on the Au Sable River during the 1800's. Rivers were a useful means of log transportation, however, this had detrimental effects on Michigan streams including loss of riparian zone vegetation, increased sedimentation, increased flashiness, breaks in connectivity, and alteration of substrate composition. Photo courtesy Lovells Township Historical Society and Glen Eberly.

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Chapter 2

Introduction

Understanding landscape effects on factors that control local stream physical habitat and biological assemblages has been evolving since it was first formally acknowledged that landscape characteristics of river valleys influence streams (Hynes 1975). A seminal work by Vannote et al. (1980) represents an early attempt to consider streams in a landscape context by classifying stream segments throughout river networks by types and sources of energy derived in part from the terrestrial environment. Frissell et al. (1986) created a hierarchical framework for defining streams on several spatiotemporal scales that acknowledged the way in which catchment factors predict conditions within stream systems from the river network down to local microhabitats of individual sites. Following an approach developed by Tonn (1990) that attempted to account for large-scale influences on fish assemblages of lakes and incorporating ideas of Frissell et al. (1986), Poff (1997) proposed a filter approach for describing landscape effects on stream systems. Poff (1997) postulated that the combination of landscape and biological filters over several scales (from the watershed to the microhabitat within a reach) could predict stream fish distributions of species based on their functional relationships. Poff (1997) also noted that in order to make filter approaches applicable, further investigation of scale-specific landscape to habitat relationships needed to be conducted. Together, these ideas underscore the importance of landscape effects in understanding mechanisms controlling habitat and biological assemblages of fluvial ecosystems and also suggest the potential relevance of considering landscape effects at different spatial scales (Wiens 2002).

Many studies have attempted to understand effects of landscape factors at different scales, focusing largely on anthropogenic land uses (Allan 2004), and both urbanization and agriculture have been shown to be strongly associated with degraded fluvial fish and macroinvertebrate communities. For example, Wang et al. (1997) found that in Wisconsin streams where the basin was dominated by agriculture, catchment land use explained the most variance in a fish index of biotic integrity (IBI) as well as metrics describing habitat condition, with increasing catchment agriculture related to declines in both biological and physical condition. Roth et al. (1996) found similar results in southeastern Michigan streams; over three spatial scales of land cover examined – the catchment, the riparian zone 1500 m upstream of the reach, and local reach riparian zone – agriculture negatively affected fish IBI and habitat index (HI) scores, with catchment agriculture showing the strongest relationship to stream conditions. In central Michigan, macroinvertebrate functional groups and species richness were more strongly related to physical habitat within a reach than to catchment agricultural land use (Richards et al. 1997). However, it was noted that high correlations between land use and surficial geology at the catchment scale may have masked effects of land use, as row crop agriculture was highly correlated with lacustrine clay geology (Richards et al. 1997). Fitzpatrick et al. (2001) found varying effects of different scales of land cover on agricultural streams in eastern Wisconsin. Fish IBI was most strongly related to land cover in the riparian buffer zone upstream of the reach and decreased with increasing human land use at that scale, while a habitat index was related to variables within the reach as well as geology at the network catchment, land cover at the reach catchment and network riparian buffer, and riparian vegetation width of the reach. Finally, streams with catchments dominated by urban land use in the Etowah River basin, Georgia, showed no significant differences in IBI or HI between reaches with forested and non-forested buffers, suggesting that urban land use in the watershed predominately influenced stream conditions (Roy et al 2003).

While relationships between anthropogenic land uses at multiple scales are known to impact stream conditions, the role of natural landscape features like geology, climate, and topography are also important. Studies have demonstrated how these factors influence both biological and physical characteristics of stream systems, and even in regions heavily impacted by human land use, the control of these factors on stream characteristics must be considered (Van Sickle and Hughes 2000). Wang et al. (2003) found that in minimally impacted catchments, species distribution and number of species are explained by in-stream physical habitat. However, Wang et al. (2003) also found that species assemblages are indirectly controlled by landscape effects on local conditions. Townsend et al. (2003) examined the influence of land use and landscape characteristics on fish assemblage, flying macroinvertebrates, and non-flying macroinvertebrates at three spatial scales, including the network catchment, the reach riparian zone, and the riffle as well as its immediate riparian zone along with in-stream conditions at the reach and riffle scale and geographic location. Fish assemblages were found to be most influenced by in-stream conditions at the reach and riffle scales, however agricultural land use in the riparian zone at these scales also had predictive power (Townsend et al. 2003). Macroinvertebrates were influenced by physical landscape conditions at the catchment scale, such as gradient and drainage area, and to a lesser extent by pasture land in the reach riparian zone. While geographic location was useful in predicting non-flying macroinvertebrate assemblages, it had no predictive power on flying macroinvertebrates.

As they show the importance of both natural and anthropogenic landscape factors summarized at multiple spatial scales in controlling stream conditions, the studies discussed above suggest that mechanisms by which landscape factors influence streams are complex. Further, they demonstrate the importance of taking a hierarchical approach when exploring landscape effects on stream conditions. One study that demonstrated the effectiveness of the hierarchical approach was Infante and Allan (in press), who quantified effects of natural and anthropogenic landscape factors summarized at the catchment scale on fish assemblage descriptors through various reach-level habitat variables to test the notion that landscape affects fish through habitat. Infante and Allan (in press) demonstrated that in their study region, physical landscape factors (e.g. drainage area and slope) did indeed have mechanistic effects on fish assemblages when acting through habitat variables. Riseng et al. (2004) also used a hierarchically-structured approach to understand the complex role of hydrologic controls and nutrient availability on macroinvertebrate functional groups through algal abundance and low and high flow disturbance metrics. Such studies performed in a hierarchical fashion allow us to better understand specifically how landscape characteristics influence streams and also develop hypotheses about the hierarchical controls on stream ecosystems as a whole.

The goal of this study is to explore how landscape factors summarized at multiple spatial scales control stream habitat conditions in northern Michigan streams. My first objective is to determine at what scale land cover variables account for the most variance in stream condition, describing a range of habitat characteristics such as habitat heterogeneity through stream reaches, reach substrate variables, descriptors of fish cover, and estimates of stream bank condition. My second objective is to evaluate how specific landscape and land cover variables affect stream habitat. To meet this objective, I used a hierarchical approach to test two specific hypotheses, 1) that land cover and land use summarized at different spatial scales should affect different characteristics of physical stream habitat and 2) that land cover variables at multiple scales have indirect effects on in-stream physical conditions through flow variability. In addressing these hypotheses, this work will provide insights into landscape and habitat interactions in my study region, and this understanding can be used to further the use of landscape ecology in stream management.

Methods

Study area

The study area includes Michigan's Upper Peninsula and the Lower Peninsula north of and including the Muskegon and Rifle River basins (Figure 2.1). Rivers within this region drain into Lakes Huron, Michigan and Superior. All sampling sites were selected from within one ecoregion as defined by the World Wildlife Fund, the Laurentian Great Lakes ecoregion (The Nature Conservancy and World Wildlife Fund 2008). The landscape of this area is dominated by managed forests, and agriculture is also present in intermittently throughout the study area (Wang et al. 2003, Danz et al. 2007).

Sixty-five study sites were selected; twenty sites in the Upper Peninsula and forty-five in the Lower (Figure 2.1). Study sites were chosen based on variation in landscape characteristics including percent wetlands, coarse geology, drainage area, and gradient, but I excluded areas with high urban development. Sites were also selected based on their accessibility, near road crossings or parks, and were located at least 1 km downstream from the first upstream tributary inflow.

Stream habitat data collection and summary

Physical habitat data were collected during the summer months of 2009 and included measures of water depth, channel shape, bank stability, riparian vegetation type, percent overhanging vegetation, substrate type and embeddedness, types and percentages of fish cover, and percentages of riffle, run, and pool habitat through study reaches.

Habitat sampling methods followed Simonson et al. (1994). Sample sites were selected upstream of the stream access point at least 10 m from stream entry, and length of the sampled area equaled 40 times average stream width (Simonson et al.1994). Each site was equally divided into 20 transects. Five point measurements of dominant substrate, depth and embeddedness were taken at regular intervals across each transect. Percent substrate including silt, sand, fine gravel, coarse gravel, cobble, boulder, bedrock and clay were visually estimated in the area occurring within 3 m of either side of the transect. Percent fish cover type measurements including macrophytes, bedrock and boulder, large woody debris (LWD), and bank undercut were estimated within the same area. Percent detritus and silt were combined into one category, "percent fines." The presence of overhanging vegetation acting as cover was recorded for both banks at each transect, as was the type and percentage of riparian vegetation or land cover within 5 m of the stream on each bank. Channel dimensions including wetted width, bankfull width, and bankfull height were also measured. Wetted and bankfull width were measured using a rangefinder accurate to 0.5 m, while bankfull height was measured using 2.5-

meter segment of PVC piping marked at 0.1 m intervals. Bankfull height, or vertical channel incision, was the measured as the difference between the elevations of the stream flow surface at the time of sampling and the point at which the stream would enter the floodplain (Infante et al. 2006). Depth coefficient of variation of pooled transect points within a site was calculated to characterize heterogeneity of depth throughout the study reach. Bank stability was visually scored for each stream bank on each transect with a score of 4 indicating a stream bank with no visible evidence of erosion, 3 indicating some evidence of erosion, 2 showing moderate erosion causing unstable soil conditions, 1 showing heavy erosion and a deteriorating bank, and 0 indicating no structural support and maximal erosion. Overall habitat conditions of the sample reach were also visually assessed using the Michigan Department of Environmental Quality (MDEQ) Procedure 51 (MDEQ 2002). This method is based on visual scores for a variety of physical characteristics used to determine stream condition and habitat quality, including embeddedness, variability in depth/velocity, flow stability, bottom deposition and sedimentation, diversity of pools, riffles and runs, bank stability, and streamside cover.

Stream flow regimes were characterized using a model of groundwater delivery to stream channels, precipitation data, surficial geology and land use (Seelbach et al. 2007). The 10/90 ratio, the annual flow that is exceeded 10% of the time divided by the annual flow exceeded 90% of the time, was calculated and used as a metric for estimating stream flow stability. A 90/50 ratio, the annual flow exceeded 90% of the time divided by the annual flow exceeded 50% of the time, was calculated to indicate areas with high baseflow (Raleigh 1982).

Landscape data

The stream coverage line data was from the 1:100,000 scale National Hydrography dataset (USGS 2004a). The basic stream unit was the confluence to confluence stream reach defined as a continuous section of surface water with similar hydrologic characteristics (USGS 2004a). Drainage area was calculated using reach catchments delineated from the NHD and the National Elevation Dataset (NED, USGS 2004b, Brenden et al. 2006). Landscape information was organized at four different spatial scales for each stream reach: local riparian zone, local watershed, network riparian zone, and network watershed (Brenden et al. 2006). Local refers to the catchment immediately surrounding and directly draining to the reach, while network refers to the area upstream of the reach through the watershed or riparian zone. The riparian zone is classified as a 60 meter buffer on either side of the stream.

Data on land cover (MNDR 2001) and surficial geology (Farrand and Bell 1982) were assembled in a previous study (Brenden et al. 2006). Stream reach gradient was the drop in meters per meters of stream reach as depicted by the NED and NHD coverages (Brenden et al 2006). Land cover types including forest, open and wooded wetlands, urban land use, and agriculture land use were then summarized as percentages at all four spatial scales.

Data analysis

I selected 22 habitat variables for analysis from an original set of 110 using both empirical and analytical procedures. Variables were transformed to achieve normality of the residuals, and variables with highly skewed residual values were excluded from further analysis. Variables with limited presence within the study region were also removed or pooled into one variable indicative of a general habitat characteristic.

Percentage variables were transformed using arcsine square root, while continuous variables were transformed using natural log. MDEQ Procedure 51 metrics did not need transformations. Pearson pairwise correlations were examined among remaining variables to help eliminate highly redundant measures determined by an r value greater than 0.6, resulting in the 22 variables broadly classified into five groups: channel flow and habitat heterogeneity, reach substrate, channel size, fish cover, and stream bank condition (Table 2.1).

The 11 landscape variables included wetlands and agriculture percent land cover at all four spatial scales and physical landscape variables including coarse surficial geology, drainage area and stream gradient (Table 2.2). Percent coarse geology was included in analysis because of its known effects on stabilizing stream flow and lowering stream temperatures (Shepherd 1989, Baker et al. 2003). This variable is the sum of geologic types with high hydraulic conductivity (k greater than 5.0 m/d), which describes the relative velocity at which water moves through porous spaces in soil (Shepherd 1989). Percent forest showed a high correlation with total wetlands at several scales (Appendix A), and because of the high correlation in these landscape factors across multiple spatial scales, I chose to eliminate forests from analysis because of the potential effect of wetlands on stabilizing stream flow regimes, sediment loading, and substrate composition (Wang et al. 2008). Percent urban land use was removed from the dataset because of its rarity throughout the study region. Box-Cox analysis was used to determine transformations for individual landscape variables to maximize normality (Legendre and Legendre 1998). Coarse geology was squared, the arcsine square root transformation was applied to agriculture at all spatial scales, and gradient was raised to the power of 0.25. Local and network riparian wetlands were normal without transformation.

My approach to understanding the effects of landscape on habitat consisted of three steps. First, a principal components analysis (PCA) was conducted on habitat variables to create principal components (PCs) that portray patterns in habitat. PCA can be useful in simplifying large multivariate datasets into a smaller number of interpretable variables (Norman and Streiner 1986, Legendre and Legendre 1998). PCA indentifies axes of variance within multidimensional space and assigns weights to individual variables to characterize the various axes. PCs can then be defined based on the variables that weight heaviest on a given axis. PCs with eigenvalues less than 1 were removed from future analysis (Norman and Streiner 1986, Legendre and Legendre 1998). PC scores for individual variables were plotted against the first four axes generated by PCA to examine potential differences in Upper vs. Lower Peninsula sites. The PCA was used only to explore possible regional difference within our study region and PC scores were not used in other multivariate analyses.

The second step was to conduct a redundancy analysis (RDA) using the program CANOCO to examine the amount of variance in habitat variables explained by each group of landscape variables. The five groups of landscape factors examined included physical landscape factors summarized in network catchments (gradient, percent coarse geology, and drainage area) and land cover variables (percent wetlands and agriculture) summarized at four spatial scales: local catchments, local riparian buffers, network catchments, and network riparian buffers of stream reaches. RDA is a direct gradient analysis that can be used to quantify variation explained in a matrix of response variables (in this case, habitat variables) by constraining their ordination to linear combinations of predictor variables (in this case, landscape factors) (Legendre and Legendre 1998, ter Braak and Prentice 1998). RDA is similar to Canonical Correspondence Analysis (CCA) but is more suitable for data that are linearly vs. unimodally distributed (ter Braak and Prentice 1998). All 22 habitat variables were included within the RDA to determine total variance in the group explained by landscape predictors. The amount of variance explained by each of the five groups of landscape predictors was determined by treating each individual group of landscape variables as predictors and treating all others as covariables (Wang et al. 2003). A biplot of the first two axes generated by the RDA was created to examine relationships among the habitat variables and landscape predictors.

For my third step, covariance structure analysis (CSA) was performed using AMOS 18.0. CSA is a multivariate technique that quantifies sources of variance in multivariate data sets (Bollen 1989, Wootton 1994, Maruyama 1998, Shumacker and Lomax 2004, Hancock and Mueller 2006). Direct effects, the influence of a predictor directly on a response variable, and indirect effects, the influences of a predictor through its relationship with a second predictor variable, can be quantified using CSA (Shumacker and Lomax 2004). The CSA model tests for the fit of the model to structure within the data, and can be used to support or refute hypotheses generated about interrelationships (Bollen 1989).

I used CSA to test the hypothesis that land cover at different spatial scales will affect physical stream habitat variables differently, both directly and indirectly by affecting stream flow regimes which I characterized by my estimate of stream flow variability (i.e., 10/90 flow ratio) (Figure 2.2). This is a technique that can be used in a hierarchical fashion to quantify relationships between a set of predictor and observed variables while also accounting for correlations between predictor variables (Bollen 1989). As it incorporates a hierarchical approach, CSA can model both direct and indirect effects of a predictor variable on a response variable (Bollen 1989). I used my model to predict all habitat variables individually and included land cover variables at scales shown to explain the most variance in habitat as supported by the RDA. Landscape variables as well as "Peninsula," an indicator variable included to broadly capture variation attributed to the location of a site in either the Lower or Upper Peninsula, were included as exogenous variables (strictly predictor variables). Ten-ninety ratio was incorporated as an endogenous variable, used to model the indirect effects of landscape variables and land cover through its effects on habitat variables (Bollen 1989). Correlation coefficients ($r>0.2$) were used to determine whether correlations should be modeled between exogenous predictor variables to account for collinearity.

Because CSA requires multivariate normality to generate reliable estimates of fit (Bollen 1989), bootstrapping was used to help achieve a higher level of multivariate normality within my dataset (Bollen 1989, Murayama 1998, Hancock and Mueller 2006). Bootstrapping is considered a reliable technique for correction of multivariate non-normality (Bollen 1989, Hancock and Mueller 2006). Maximum likelihood was the estimation technique used in my model, as it tends to be robust to deviations from normality (Bollen 1989, Hancock and Mueller 2006).

Twenty-two separate runs of the model were conducted for each habitat variable, and indices of overall fit and parsimony of the model were selected following previous studies (e.g., Riseng et al. 2004, Infante and Allan in press). Indices of fit were Chi-square ($P > 0.05$), root mean square error of approximation (RMSEA $P < 0.05$), Tucker-Lewis Index (TLI>0.9) and Normed Fit Index (NFI>0.9). If the model was determined to be significant, percent observed variance explained (r^2) as well as direct and total effects and their significance ($P<0.05$) were evaluated for each habitat variable.

Results

Landscape and in-stream habitat conditions

Study site drainage area ranged from 7 to 716 km^2 (Table 2.2). Reach gradient varied by two orders of magnitude, from 0.0001 to 0.0178. Catchments had relatively low levels of human land disturbance compared to southern Michigan; the highest mean value over all scales of agriculture was 5.18%. Wetlands were present at all scales and reached values of over 80% in the network and local riparian zone. Coarse geology was dominant throughout study catchments, with a mean value of 84.83%.

Habitat characteristics varied throughout the study sites (Table 2.1). While runs were the dominant habitat type, riffles had a mean of 13% and a maximum value of 70%. Pools were less common with a maximum of only 17%. Stream flow regimes varied across the study region as indicated by multiple variables. Stream flow stability, a visual estimate, ranged from 2 to 10 (maximum possible stability score), and the 10/90 ratio ranged from 1.13 to 47.92. Sand was the most dominant substrate type with a mean of 45% across all sites. Fine gravel was less common in sites with a mean of 9% and maximum of 46%. Wetted width varied greatly, ranging from 2.90 to 38.38 m. Overhanging vegetation had a mean of 43% and a maximum value of 100%. Overall, stream bank condition ranged from moderately poor to very good, indicated by visual measures of bank stability. Bank stability averaged across all sites was 3.19, suggesting that erosion and scouring are uncommon in my study streams.

Patterns of in-stream habitat conditions

PCA of twenty-two habitat variables generated four principle components explaining 65% of the variance in habitat data (Table 2.3). Axis 1 explained 27% and was positively weighted by the presence of riffle habitat; coarse substrate, rock cover – which includes cobble, boulder, and bedrock – and high interstitial spacing scores, while runs weighted negatively on the axis. For these reasons, I named this axis "riffle system habitat and coarse substrate," although it indicates a range in substrate and habitat types. Axis 2 explained 15% of the variance in habitat variables, and indicated a range in the variability of stream flows. Stream flow stability, a visually estimated-variable, weighed heavily on the axis, as did bank stability. Bankfull minimum height weighted negatively. Axis 3 was positively weighted by 90/50 ratio, average depth, and wetted width, indicating that the axis was representative of larger streams. This axis explained 12% of the variation. The fourth axis was only heavily weighted by pools, again, relatively uncommon in my study sites, and explained 9% of the variance in habitat data.

Sites scores plotted against axes generated by PCA showed that some characteristics differed across peninsulas. While no difference was detected in amounts of riffle habitat and coarse substrate (Figure 2.3B), streams in the Lower Peninsula tended to be larger than those in the Upper Peninsula (Figure 2.3A). Also, site scores plotted against axes 1 and 2 indicate that stream stability differs by peninsula (Figure 2.3A). Seventeen of twenty Upper Peninsula sites (85%) fell below the x axis, indicating that these streams were less stable than many Lower Peninsula streams. Stream stability in the Lower Peninsula varied, but tended to be more stable overall. Because of the differences in stability and stream size across peninsulas, an indicator variable was included in the CSA model to account for those regional differences, with 1 indicating the Lower Peninsula and 0 indicating the Upper Peninsula.

Relationships between landscape and habitat variables

The RDA indicated that site scale habitat conditions were associated with landscape variables at multiple scales. Together, the fifteen predictor variables explained 41% of total variance in habitat variables (Figure 2.4). The physical landscape grouping accounted for most of the explained variance (57%), and land cover in the network riparian zone accounted for 13%. Local riparian zone land cover explained just over 5%, slightly more than the network watershed. The local watershed land cover explained the least variance, with only 1% accounted for.

A biplot of habitat and land cover variables in multidimensional space depicted across two generated RDA axes indicates differences in landscape to habitat relationships that may be related to the scale at which a land cover variable was quantified (Figure 2.5). The lengths of vectors, representative of landscape variables, indicate the weight of the individual variable on the habitat dataset. Drainage area, gradient, network riparian wetlands, local riparian wetlands, and percent coarse geology have the most weight on habitat variables. Habitat variables in close proximity to landscape variables are highly positively correlated with said landscape variables, those at ninety degrees angles are maximally uncorrelated, and those opposite landscape variables are maximally negatively correlated. Drainage area and gradient are highly correlated with habitat variables indicative of riffle systems and larger streams; habitat heterogeneity, coarse substrate, wetted width, coarse gravel, and bedrock and boulder that can act as stream cover. Drainage area and gradient are highly negatively correlated with runs, fine substrate, macrophytes and overhanging vegetation, while these habitat variables are positively correlated with local riparian wetlands.

Coarse geology and network riparian wetlands are positively correlated with indicators of flow stability (stream flow stability, bank stability) and increased baseflow (90/50 flow ratio), while negatively correlated with indicators of instable flows (10/90 ratio, minimum bankfull height). Local and network catchment wetlands weight weakly on the dataset, while wetlands at different scales correlate differently with habitat variables.

The CSA model

My approach in developing the CSA model was to compare the influence of different landscape factors on stream habitat, including the influence of landscape factors summarized at multiple scales. I used results of the PCA and RDA as well as correlations among landscape factors to aid in model development. Given the relatively large amount of variance (57.8%) that they accounted for out of the total variance explained (41.2%), all physical landscape variables including coarse geology, catchment area, and gradient were incorporated into my model as exogenous variables (Figure 2.2). However, landscape variables summarized in the network watershed and local watersheds of my study sites were excluded because each grouping was found to account for less than 5% of the total explained variance with the RDA. In contrast, landscape variables summarized at the scales of the local and network riparian zones explained 13.1% and 5.3% respectively and were included in the models. Besides these natural and anthropogenic landscape factors, I also included the indicator variable "Peninsula" to broadly capture regional differences in controls on stream systems.

In assigning relationships within my model, agriculture and wetlands in the local riparian zone, wetlands in the network riparian zone, and drainage area were modeled to have both direct and indirect effects on habitat variables. Both the indicator variable "Peninsula" and gradient were modeled as having direct effects on habitat variables. Percent coarse geology was modeled as having only indirect effects on habitat due to the strong influence of geology on Michigan stream flow regimes (Seelbach et al. 2007).

CSA results

All models predicting individual habitat variables were significant based on my set of fit statistics except for the model predicting 90/50 flow ratio (Table 2.5). Therefore, all models except for that predicting the 90/50 flow ratio were considered. Two out of the remaining twenty-two models predicting fine gravel and percent pools showed no significant relationships between predictors and habitat data and explained low amounts of variation ($r^2 < 0.10$).

Effects of landscape on flow stability

Two of the five variables modeled to influence 10/90 ratio were found to have significant direct effects (Table 2.6). Both were physical habitat variables, drainage area and percent coarse geology, and the 10/90 flow ratio decreased as these variables increased indicating more stable stream flow regimes. The r^2 value for the 10/90 flow ratio was 0.72, indicating that a majority of variance in this factor was explained by the model. Neither agriculture nor wetlands in local or network riparian zones had a significant effect on the 10/90 ratio.

Effects of landscape variables on in-stream habitat

Natural landscape variables significantly affected many habitat variables (Table 2.7), with direct effects very similar to total effects (Table 2.8). Local riparian agriculture had no significant effects on any stream habitat variable. Wetlands in both the local and network riparian zone were found to have different effects on habitat variables indicative of stream stability, substrate type, and habitat heterogeneity.

Variables describing channel flow and habitat heterogeneity generally had r^2 values ranging from 0.36 to 0.48, with the exception of percent pools which was poorly predicted by the model. Both runs and riffles decreased with increasing drainage area and gradient, while the 10/90 flow ratio was negatively associated with stream flow stability. Coarse geology was positively associated with the visual estimate of stream flow stability, and study sites in the Lower Peninsula were shown to be more stable. Local riparian zone wetlands had no significant effects on any habitat variables within this group. Network riparian zone wetlands had negative effects on runs and depth coefficient of variation and were positively related to stream flow stability and riffle habitat.

Overall amounts of variation explained in substrate variables were fairly high (r^2 = 0.37-0.47) with the exception of fine gravel. Reach substrate generally increased in size with increasing drainage area and gradient, while coarse substrate, which included boulder and bedrock, decreased as coarse surficial geology increased in catchments of the study region. Sand was less common in systems with variable stream flow regimes, while coarse substrate increased as flow stability decreased. As wetlands in the network riparian zone increased, substrate size also generally increased, but this variable was not shown to have a significant effect on fine substrate. Local riparian zone wetlands were negatively correlated with the presence of coarse gravel.

Average depth and wetted width were well predicted by my model, and over 68% of the variance was explained for depth. Drainage area had a large direct effect on wetted width (0.81), while network riparian wetlands and 10/90 ratio had a weaker positive effect.

Fish cover variables were only significantly predicted by drainage area, gradient and the 10/90 flow ratio with explained variance ranging from 21% to 35%; this was the lowest of all habitat variable groupings. Larger streams were associated with decreases in cover variables except rock cover (BED) which increased significantly with drainage area (total effect of 0.29). Increases in boulders and bedrock that could supply fish cover were also significantly associated with increased gradient and 10/90 ratio. Macrophytes decreased with increasing gradient and drainage areas. Local riparian wetlands had no significant effects on macrophytes.

Variables describing stream bank condition were well predicted by the models. Bank stability and minimum bankfull height had 53% and 60% of their variation explained, respectively. The visual metric describing riparian vegetation type and condition decreased with larger drainage areas and was generally of higher quality in the Lower Peninsula. Bank stability increased as 10/90 ratio decreased and as coarse geology increased, and it has a positive but insignificant relationship with network riparian wetlands. Minimum bankfull height significantly decreased in stable streams with network riparian zone wetlands, but showed no relationship with local riparian zone wetlands.

Discussion

Overview

My analyses demonstrated ways in which landscape factors relate to stream habitat, including how factors summarized at different spatial scales predict different habitat characteristics. By using ecological understanding of landscape to habitat relationships along with results of a multivariate analysis (RDA), I developed a CSA model to test hypotheses about the response of habitat to landscape predictors at multiple spatial scales in my study region. My first hypothesis, that land cover and land use summarized at different spatial scales should affect different characteristics of physical habitat, was supported. I found that wetlands in the network riparian zone were associated with increases in stream flow stability and substrate size, while wetlands in the local riparian zone were negatively associated with increasing amounts of coarse gravel and not significantly associated with any of the other habitat characteristics that I considered. Agriculture in the local riparian zone had no significant effects on habitat conditions; however, natural landscape variables including percent coarse surficial geology, drainage area, and gradient significantly affected many of the habitat variables. Despite being strongly affected by coarse geology and drainage area, the 10/90 flow ratio was not significantly affected by any of my land cover variables, and this finding failed to support my second hypotheses. I conclude that in my study streams, natural landscape variables are closely associated with stream habitat; wetlands at the network riparian zone scale are secondary predictors of habitat heterogeneity, substrate size and stream flow stability; and local riparian wetlands have minimal effects. By understanding specific effects of land cover at multiple scales in natural systems, we can more appropriately incorporate landscape analyses into management and conservation practices.

Physical landscape controls on stream habitat

My results indicate that drainage area, gradient, and geology have the strongest effects on physical conditions of my study streams. Drainage area had a significant positive effect on habitat heterogeneity, larger substrate, and riffle habitat, a result that may be due to an increase in stream power with greater catchment area. Stream power increases with greater stream flows which can increase with drainage area. More stream power provides streams more opportunity to do work, potentially leading to greater variability in depth, greater diversity in habitat types present, and increased movement of fine substrate compared to smaller streams (Hauer and Lamberti 1996, Knighton 1998). Drainage area's significant negative relationship with LWD may be caused by the effect of stream power, increasing movement of wood through the stream. Drainage area also had significant negative effects on the presence of overhanging vegetation, and the presence of overhanging vegetation and LWD were positively correlated (r^2= 0.27). Less overhanging vegetation in a reach may indicate a decreased presence of woody plants within the riparian zone, potentially lessening LWD input into the stream. Another reason for drainage area's significantly negative relationship with LWD may be that I did not account for stream size differences when calculating my LWD measurements within the transect. It is possibly that the trend of decreasing LWD with increasing drainage area may be caused by the relatively larger wettedvwidth in larger drainage areas, meaning that if a small stream has the same amount of LWD as a large one, the percentage of the stream containing LWD may be greater in the stream with a smaller wetted width.

Controlling for stream size may better demonstrate how LWD may be affected by drainage area.

Stream gradient had similar relationships to habitat conditions as drainage area, and was significantly related to increases in habitat heterogeneity, substrate size, and riffle habitat. Increased gradient is related to increased stream power within a system (Knighton 1998). However, in my study region, stream gradient and drainage area are strongly negatively correlated (r^2= -0.59). A study conducted in southeast Michigan found similar effects of drainage area and gradient on habitat heterogeneity, riffle presence and substrate, postulating that maximum stream power was achieved in medium-sized streams of the study region where drainage area and gradient were maximized (Infante and Allan in press). Southeast Michigan is an area of comparatively heavy human disturbance while surficial geology varies from regions dominated by coarse materials to areas dominated by clay and sand lakeplain (Infante and Allan in press). Similar findings on the role of drainage area and gradient on stream habitat despite differences in land cover and surficial geology across northern vs. southern Michigan demonstrates that gradient and drainage area are important drivers of substrate type and channel habitat heterogeneity in multiple systems.

My results are consistent with other recent work in the region by Wang et al. (2003) who found that natural landscape factors including drainage area and surficial geology at the network catchment scale explained much of the variance in stream habitat variables including channel morphology, substrate type, and assessments of dissolved oxygen, conductivity, pH, alkalinity, hardness and turbidity. The role of natural landscape variables in the network catchment in an overlapping study region emphasizes the importance of considering these variables when attempting to predict stream conditions.

Increasing coarse surficial geology was associated with lower 10/90 flow ratios within my study region. In Michigan, surficial geology has been shown to have major effects on stream flow and temperature regimes through effects on groundwater delivery (Seelbach and Wiley 1997). Surficial geology was found to have limited effects on other factors examined in this study, but its significant negative relationship with coarse substrate may be indicative of its control on substrate type within a reach. Areas with small amounts of coarse geology are more prone to high flow events and therefore increased stream power, which would move fine sediments and smaller substrate to lower reaches or out of a system, potentially increasing the percentage of coarse substrate within the stream.

The lack of a significant effect of land cover on 10/90 ratio may be due to the fact that land cover, specifically wetlands, may be influencing different characteristics of catchment hydrology than that captured by the 10/90 flow ratio, a ratio quantifying annual high over annual low flows. Perhaps a more seasonal measure, such as spring or fall high flow events controlled for by drainage area, may indicate wetlands having a more direct effect on attenuation of flows. Similarly, my failure to detect effects of agriculture on the 10/90 flow ratio may be due to the fact that agriculture was relatively uncommon throughout my study region and its influence was not readily detectable.

General effects of land cover at different spatial scales: watershed versus riparian zone

The RDA results indicate that land cover in the riparian zone explained some variance in my group of stream habitat characteristics, while watershed land cover explained comparatively little variance within the dataset. This result suggests that riparian zone land cover is more useful in predicting habitat conditions than catchment area land cover in my study region, and the CSA confirms that wetlands in the riparian zone do explain significant amounts of variance in habitat heterogeneity, flow stability, and substrate percentage.

Network catchment land cover has been shown to be the strongest predictor of stream habitat condition in several studies of systems dominated by human land use including urban, agriculture, or a combination of both (Roth et al. 1996, Wang 1997, Roy et al. 2003, Stephenson and Morin 2009). While these studies examine different regions and a variety of landscape conditions, they all focus on areas of heavy anthropogenic disturbance. My study region is different in that it focuses on areas with minimal current human impact. My results indicate that land cover in network riparian zone explains a larger amount of variance within stream habitat conditions in systems dominated by natural conditions. Wang et al. (2003) found similar results in a study region encompassing much of northern Wisconsin and a portion of my study region, an area dominated by natural conditions, stating that the local riparian zone land cover explained more variance than network catchment land cover overall. The results of Wang et al. (2003) and my study compared to studies with largely disturbed catchments suggests that as a watershed is increasingly disturbed through human land use, the effects of the modified catchment on stream stability, habitat heterogeneity and substrate type may outweigh the effects of the network riparian zone.

While wetlands at the catchment scale were positively associated with RDA Axis 2, suggesting a relationship with stream instability, they were not included in my CSA model because of the relatively low amount of variance explained in my set of habitat variables by watershed land cover in general. In contrast, riparian zone wetlands were negatively associated with RDA Axis 2, suggesting a relationship with increased stream flow stability. In the Tittabawasee River system, Michigan, catchments with greater than 60% wetlands, including forested and open water wetlands, were shown to have lower flow stability and greater total water yield compared to those with less wetlands (Tompkins et al. 1997). However, Tompkins et al. (1997) did not examine the role of wetlands in the riparian zone. While my results did not contradict Tompkins et al. (1997), I saw a different effect of wetlands when summarized at the network riparian zone versus the catchment scale. The results of my study emphasize that the scale at which landscape is quantified in a study can lead to potentially differing conclusions about controls on habitat condition.

Specific effects of network and local riparian wetlands on habitat

Wetlands summarized at the network vs. local riparian zones had significantly different effects on reach substrate, responses to flow stability, and habitat heterogeneity. Network riparian zone wetlands had a significant negative effect on bankfull minimum height and a significant positive effect on the visual metric of stream flow stability. Together, these results indicate that at the network riparian zone, wetlands may be acting to mitigate high, channel shaping stream flows, absorbing surface runoff and rainwater and pooling it for increased periods of time (Cohen and Brown 2007, Wang et al. 2008). Also, wetlands in the network riparian zone have greater control over catchment hydrology influencing a particular reach than wetlands at a local scale. A recent Florida study focused on modeling the effectiveness of wetlands at multiple scales at removing sediment and attenuating flow for storm water removal (Cohen and Brown 2007). While local headwater wetlands had small effects on decreasing flood levels, in a system containing the same percentage of wetlands located throughout the stream network, the intensity of storm flows was lowered to an even greater degree (Cohen and Brown 2007).

My results also suggest that network riparian wetlands may be affecting reach substrate. Wetlands are known to trap sediments and fine particles delivered from upstream catchment areas, therefore reducing fine sediment presence within the stream (Johnston 1991, Cohen and Brown 2007, Wang et al. 2008). In my study area the network riparian zone wetlands may be affecting stream substrate in this way, a result that is supported by their significantly positive relationship with riffle habitat. Because network riparian zone wetlands were not significantly correlated with drainage area or gradient, other variables significantly affecting hydrology, its control on substrate occurs independently. I failed to see an effect of wetlands on fine substrate, however this may be because I grouped sediment and detritus in my analysis. Detritus, decaying masses of organic material, is very common in areas dominated by wetlands, while fine sediment has been shown to be removed by wetlands in the riparian zone (Tompkins et al 1997, Wang et al. 2003, Wang et al. 2008). By pooling these two substrates types into one category, I may have masked the influence of wetlands on fine sediments. In contrast, local riparian zone wetlands have a significantly negative effect on the presence of coarse gravel, leading us to the conclusion that wetlands at these two scales impact stream substrate composition in a different way. In minimally impacted streams of Wisconsin and some of northern Michigan, the effects of local riparian wetlands was the best single predictor of substrate compared to watershed landscape and land cover conditions as well as other local riparian land cover, but the network riparian zone was not assessed (Wang et al 2003). The Florida study on the effects of multiple scales of wetlands that predicted decreases in flood intensity with network versus local wetlands also predicted that wetlands throughout the network were more effective than local riparian wetlands at removing sediments within the stream (Cohen and Brown 2007).

Utility of CSA and RDA

By combining these two multivariate analytical technique (RDA and CSA), I was able to develop and test hypotheses suggested by actual relationships within my data to account for variance explained at multiple scales. RDA biplots allowed for a visualization of how patterns in habitat conditions may be related to patterns in landscape, including landscape factors expressed at multiple scales. RDA was also a useful tool in creating the CSA model by allowing me to assess which landscape scale groupings explained the most variance in habitat factors. While RDA allowed for the examination of broad relationships between sets of landscape factors and habitat variables, it does not allow for examining specific relationships among pairs of variables or tests of significance. Due to the nature of the biplots that I generated, which represent a compression of multidimensional space down to two axes, interpretations of results must be made cautiously. While a habitat variable may be associated with a certain landscape variable in the biplot, it does not mean that a causal relationship exists. The RDA biplot (Figure 2.4) shows that local riparian zone wetlands are associated with habitat variables like riparian vegetation condition, sand, fine substrate and macrophytes. However, when each habitat variable was independently examined within the CSA model, my results showed that drainage area and gradient are actually the strongest predictors within the dataset, located at the opposite end of Axis 1.

The value of CSA is that it allows for the examination of specific effects of landscape predictors on habitat variables while accounting for correlations among the predictors (Bollen 1989). CSA also allows for the assessment of significance of effects on a particular habitat variable, so one can then understand which predictors are strongly acting upon the predicted variable, which is not available through multivariate approaches like RDA.

Implications

My study area has a unique history associated with its landscape. While today the region is largely forests and wetlands, in the late 1800's and early 1900's much of the land was altered through logging (Mershon 1923, Maybee 1960, Vincent 1962, Dickmann and Leefers 2003). The streams were the main artery for the transport of logs, which were piled on cleared riparian areas until spring at which time they were pushed down river during high seasonal flows (Dickmann and Leefers 2003). Stream systems were altered significantly in terms of substrate, channel morphology and hydrologic conditions through these intense disturbances (Vincent 1962, Miller 1966, Dickmann and Leefers 2003, Johnson et al. 2003). Gravel riffles were scoured by the driving of logs and covered with sand deposited from the surrounding watershed, while channels were deepened and widened and woody debris was lost, reducing overall channel complexity and permanently altering the streams (Maybee 1960, Vincent 1962). Harding et al. (1998) found that catchments dominated by agriculture in the 1950's now dominated by second growth forests still showed macroinvertebrate assemblages similar to those catchments currently dominated by agriculture. In my study region, it is possible that some of the unexplained variance in my dataset could be attributed to the historical alterations of catchments. For instance, while network riparian wetlands are correlated with most substrate conditions, fine gravel is not significantly related to this variable. Fine gravel's very low r^2 value (0.09), lack of any significant predictors, and limited presence within the study area suggests that it is not well predicted by variables within my model. It is possible that the increases in substrate deposition in the form of sand from former periods of high erosion and runoff may have altered stream systems so that areas historically dominated by fine gravel are now dominated by sand, therefore causing the variable to be poorly predicted by landscape predictors.

While the unique characteristics of my study region may limit the application of my results beyond this ecoregion, these results supply a base for considering similar questions in other regions. For instance, Utz et al. (2010) showed that even within a relatively small area of coastal Maryland, variations in physical landscape attributes across regions within the same stream systems can cause a change in the effect of urban land cover on fish assemblages. By comparing studies and results across regions, we can develop a deeper understanding of the complexities of landscape control on habitat conditions while looking for broad, overarching relationships that may exist despite regional differences.

My study supports the theory that the landscape affects stream habitat at multiple scales (Poff 1997, Allan 2004, Wiens 2002). By understanding the specific relationships between landscape at different scales and habitat conditions, I can apply hierarchically-structured approaches to identify suitable habitat for species and to better understand stream community assemblage. To apply methods like the filter approach within the stream as described by Poff (1997) in largely natural systems, a greater understanding of controlling landscape factors is needed in these regions. Identifying which scale of natural land cover affects habitat conditions like substrate composition, flow stability, and habitat type can be useful in predicting stream reaches that may have conditions that are suitable for spawning, feeding and refuge sites for fish species (Fausch et al. 2002, Durance et al 2006). With greater understanding of controlling factors in a region, we can improve the results of such an analysis and conduct studies quickly and efficiently using the growing amount of landscape and land cover data available across the United States.

The identification of landscape and land cover effects at multiple spatial scales also has direct benefits for management. For example, my study demonstrated that at the network riparian zone scale, wetlands have a more significant effect on the limitation of fine sediments within the stream than at any other scale. Managers considering the use of wetlands for sediment control could benefit from this information when deciding how and where wetlands could be constructed within a stream system. Similarly, I concluded that network riparian zone wetlands play a role in stabilization of flows within the stream, while local riparian wetlands have a limited effect on attenuating flow and catchment wetlands may contribute to flow instability. Managers hoping to use wetlands to attenuate flow can use studies such as this as a guide, and avoid adversely affecting stream stability by constructing wetlands at other scales. Overall, my work accentuates the point that when attempting to manage stream systems through the alteration of land cover or when trying to identify stream conditions based on the landscape approach, the scale at which land cover is summarized must be considered, even in largely natural systems.

Table 2.1: Mean, range and standard deviation of habitat variables used in analyses.

Category	Variable name	Code	Mean	Range	Standard deviation
Channel flow and habitat heterogeneity					
	Pools (%)	Pool	3.00	0.00-17.00	4.00
	Riffles (%)	Rif	13.00	0.00-70.00	19.00
	Run (%)	Run	84.00	30.00-100.00	19.00
	Depth coefficient of variation	DCV	0.46	0.22-0.98	0.15
	Habitat heterogeneity	HH	12.45	6.00-20.00	4.17
	Stream flow stability	SFS	7.12	2.00-10.00	2.19
	10/90 flow ratio	10/90	5.18	1.13-47.92	6.09
Reach substrate					
	Fine substrate (%)	FS	11.00	0.00-54.00	12.00
	Sand (%)	SD	45.00	0.00-94.00	31.00
	Fine gravel (%)	FG	9.00	0.00-46.00	11.00
	Coarse gravel (%)	CG	22.00	0.00-74.00	24.00
	Coarse substrate (%)	CS	13.00	0.00-78.00	20.00
Channel size					
	90/50 flow ratio	9050	0.55	0.19-0.97	0.13
	Average depth (cm)	DEP	50.63	11.06-132.75	23.82
	Wetted width (m)	WW	12.78	2.90-38.38	7.17
Fish cover					
	Undercut (%)	UNC	1.00	0.00-7.00	1.00
	Boulder or bedrock (%)	BED	1.00	0.00-14.00	3.00
	Large woody debris (%)	LWD	10.00	0.00-34.00	7.00
	Macrophytes (%)	MAC	5.00	0.00-27.00	7.00
	Overhanging vegetation (%)	OV	43.00	2.50-100.00	21.00
Stream bank condition					
	Riparian vegetation	RV	8.16	3.00-20.00	1.67
	Bank stability	BS	3.19	2.18-4.00	3.70
	Minimum bankfull height (cm)	HM	59.29	4.50-272.50	47.12

Table 2.2: Mean, range and standard deviation of landscape variables used in analyses

Category	Variable name	Code	Mean	Range	Standard deviation
Physical landscape					
	Coarse geology in network watershed (%)	Coarse	84.83	0.00-100.00	27.01
	Gradient of stream reach	Gradient	0.0022	0.0001-0.0178	0.00
	Drainage area (km²)	DA	127.17	6.69-715.55	134.75
Network riparian					
	Agriculture in the network riparian (%)	NRAg	2.93	0.00-30.28	5.11
	Wetlands in the network riparian (%)	NRWet	44.81	4.60-82.90	18.04
Network watershed					
	Agriculture in the network watershed (%)	NWAg	5.17	0.00-23.64	6.13
	Wetlands in the network watershed (%)	NWWet	18.90	1.91-73.05	13.60
Local riparian					
	Agriculture in the local riparian (%)	LRAg	1.81	0.00-17.78	3.81
	Wetlands in the local riparian (%)	LRWet	50.03	7.03-82.9	20.64
Local watershed					
	Agriculture in the local watershed (%)	LWAg	4.12	0.00-27.42	6.48
	Wetland in the local watershed (%)	LWWet	17.38	1.91-65.74	13.29

Table 2.3: PCA results of 22 habitat variables. Four axes explained 65.05% of the variation in habitat data. Bold values indicate variable weights with an absolute value greater than 0.6 that were used to interpret individual axes.

	Axis 1 Riffle systems and coarse substrate	Axis 2 Responses to flow stability	Axis 3 Stream size	Axis 4 Pools and overhanging vegetation
% Variance explained	**27.15**	**15.70**	**12.23**	**9.25**
Code				
Rif	**0.90**	-0.10	-0.15	0.00
CS	**0.80**	-0.16	-0.14	-0.08
CG	**0.77**	0.00	0.20	-0.12
BED	**0.62**	-0.21	-0.23	-0.09
SD	**-0.88**	-0.06	0.09	0.31
Run	**-0.89**	0.08	0.19	-0.15
SFS	-0.06	**0.87**	0.12	0.01
BS	0.09	**0.82**	0.05	0.03
DCV	0.26	**-0.62**	-0.35	-0.22
HM	0.09	**-0.90**	0.00	-0.03
WW	0.08	-0.06	**0.81**	-0.37
90/50	-0.11	0.40	**0.74**	-0.13
DEP	-0.25	0.15	**0.81**	-0.01
Pool	0.20	-0.12	-0.09	**0.61**
OV	-0.22	0.21	0.00	**0.73**
HH	0.50	-0.28	0.51	0.18
UNC	0.08	0.08	-0.23	-0.02
FG	-0.07	-0.01	0.45	-0.12
RV	-0.16	0.42	-0.21	0.52
LWD	-0.33	-0.27	-0.16	0.45
MAC	-0.35	0.53	-0.20	-0.28
FS	-0.50	0.17	-0.52	-0.24

Table 2.4: Pearson pairwise correlations for landscape variables used in CSA. Variables with correlations higher than an absolute value of 0.2 are shown in bold and were included in the model.

	DA	LRWet	NRWet	Gradient	Coarse	LRAg	10/90	Peninsula
DA	1.00							
LRWet	0.18	1.00						
NRWet	0.05	**0.46**	1.00					
Gradient	**-0.59**	**-0.49**	**-0.23**	1.00				
Coarse	0.11	-0.06	-0.18	-0.02	1.00			
LRAg	-0.11	**-0.23**	**-0.23**	-0.01	-0.05	1.00		
10/90	**-0.59**	**-0.22**	-0.05	**0.36**	**-0.65**	0.18	1.00	
Peninsula	**0.23**	**0.21**	0.11	**-0.29**	**0.46**	0.01	**-0.41**	1.00

Table 2.5: Fit statistics for CSA models predicting habitat variables from landscape factors. Statistics include Chi-square goodness of fit (X^2), root mean square error of approximation (RMSEA), Tucker-Lewis Index (TLI) and Normed Fit Index (NFI). Fit of each model is indicated by "yes" or "no."

Category	Variable	X^2	X^2 p	RMSEA	TLI	NFI	Fit?
Channel flow and habitat heterogeneity							
	Pool	10.89	0.62	0.00	1.04	0.94	Yes
	Rif	11.4	0.59	0.00	1.02	0.95	Yes
	Run	11.21	0.59	0.00	1.02	0.95	Yes
	DCV	12.37	0.5	0.00	1.01	0.95	Yes
	HH	12.65	0.48	0.00	1.01	0.94	Yes
	SFS	11.41	0.58	0.00	1.02	0.95	Yes
Reach substrate							
	FS	15.07	0.3	0.05	0.97	0.93	Yes
	SD	11.7	0.55	0.00	1.02	0.95	Yes
	FG	12.04	0.52	0.00	1.02	0.94	Yes
	CG	10.9	0.62	0.00	1.03	0.95	Yes
	CS	10.9	0.62	0.00	1.03	0.95	Yes
Channel size							
	9050	1.9	0.03	0.12	0.91	0.94	No
	DEP	11.82	0.54	0.00	1.01	0.96	Yes
	WW	13.27	0.43	0.02	1.00	0.96	Yes
Fish cover							
	UNC	10.95	0.62	0.00	1.03	0.95	Yes
	BED	12.07	0.52	0.00	1.01	0.94	Yes
	LWD	10.94	0.62	0.00	1.03	0.95	Yes
	MAC	11.21	0.59	0.00	1.03	0.95	Yes
	OV	15.38	0.29	0.05	0.96	0.92	Yes
Stream bank condition							
	RV	11.16	0.6	0.00	1.03	0.95	Yes
	BS	10.93	0.62	0.00	1.03	0.95	Yes
	HM	10.98	0.61	0.00	1.03	0.96	Yes

Table 2.6: Standardized total effects generated through CSA of landscape factors on 10/90 flow ratio. Significant effects are shown in bold (*P*<0.05).

Landscape factors	10/90 flow ratio
Drainage area	**-0.49**
Coarse geology	**-0.62**
LRAg	0.06
LRWet	-0.14
NRWet	0.06
r^2	0.72

Table 2.7: Standardized total effects generated through CSA of landscape variables on individual habitat variables. Effects that are statistically significant ($P<0.05$) are shown in bold.

Category	Variable	r^2	Standardized total effects				
			Drainage Area	Gradient	Coarse	Peninsula	10/90
Channel flow and habitat heterogeneity							
	P	0.07	-0.24	-0.06	-0.03	-0.03	0.04
	Rif	0.41	**0.40**	**0.77**	-0.11	0.01	0.18
	Run	0.36	**-0.30**	**-0.68**	0.11	0.01	-0.18
	DCV	0.47	0.08	**0.25**	-0.02	**-0.52**	0.05
	HH	0.35	**0.61**	**0.40**	0.11	-0.14	-0.17
	SFS	0.48	**-0.14**	0.00	**0.27**	**0.34**	**-0.44**
Reach substrate							
	FS	0.37	**-0.69**	**-0.62**	-0.04	0.08	0.07
	SD	0.44	**-0.49**	**-0.65**	0.17	-0.07	**-0.28**
	FG	0.09	0.18	-0.04	0.08	0.08	-0.13
	CG	0.43	**0.56**	**0.58**	-0.03	0.07	0.05
	CS	0.47	**0.47**	**0.58**	**-0.27**	-0.08	**0.43**
Channel size							
	DEP	0.68	**0.50**	**-0.34**	0.14	**0.16**	**-0.23**
	WW	0.84	**0.90**	-0.01	0.11	-0.10	**-0.18**
Fish cover							
	UNC	0.21	-0.25	0.17	-0.15	0.19	0.23
	BED	0.35	**0.29**	**0.41**	-0.18	-0.22	**0.30**
	LWD	0.24	**-0.39**	-0.10	0.10	-0.23	-0.17
	MAC	0.24	**-0.44**	**-0.57**	0.04	0.02	-0.07
	OV	0.17	**-0.43**	-0.28	0.11	0.00	-0.18
Stream bank condition							
	RV	0.27	**-0.44**	-0.11	0.05	**0.30**	-0.08
	BS	0.53	-0.15	0.13	**0.32**	**0.45**	**-0.52**
	HM	0.60	**0.34**	0.10	**-0.18**	**-0.57**	**0.29**

Table 2.7: Continued

Category	Variable	LRAg	LRWet	NRWet
Channel flow and habitat heterogeneity				
	P	-0.05	-0.16	0.10
	Rif	0.09	0.03	**0.23**
	Run	-0.05	0.04	**-0.25**
	DCV	0.01	-0.04	**-0.24**
	HH	0.15	-0.10	0.06
	SFS	0.02	0.10	**0.34**
Reach substrate				
	FS	-0.03	-0.07	-0.16
	SD	0.02	0.18	**-0.33**
	FG	-0.01	-0.06	-0.11
	CG	0.01	**-0.26**	**0.21**
	CS	0.10	-0.09	**0.36**
Channel size				
	DEP	0.02	-0.10	0.08
	WW	0.01	-0.08	**0.14**
Fish cover				
	UNC	-0.21	0.05	-0.13
	BED	0.06	-0.16	0.14
	LWD	0.22	0.10	-0.06
	MAC	-0.15	-0.08	0.05
	OV	0.03	0.01	0.09
Stream bank condition				
	RV	-0.19	0.07	-0.16
	BS	-0.05	-0.04	0.15
	HM	0.10	0.02	**-0.27**

Table 2.8: Standardized direct effects of landscape variables generated through CSA on individual habitat variables. Effects that are statistically significant ($P<0.05$) are shown in bold.

Category	Variable	Standardized direct effects						
		Drainage Area	Grad -ient	Peninsula	LRAg	10/90	LRWet	NRWet
Channel flow and habitat heterogeneity								
	P	-0.22	-0.06	-0.03	0.00	0.04	-0.16	0.10
	Rif	**0.49**	**0.77**	-0.02	0.09	0.18	0.05	**0.24**
	Run	**-0.39**	**-0.68**	0.01	-0.05	-0.18	0.01	**-0.26**
	DCV	0.10	**0.25**	**-0.52**	0.01	0.03	-0.03	**-0.24**
	HH	**0.52**	**0.40**	-0.14	0.15	-0.17	-0.12	0.05
	SFS	**-0.36**	0.00	**0.34**	0.02	**-0.44**	0.04	**0.31**
Reach substrate								
	FS	**-0.65**	**-0.62**	0.07	-0.03	0.07	-0.06	-0.15
	SD	**-0.63**	**-0.65**	-0.07	0.02	**-0.28**	0.14	**-0.35**
	FG	0.12	-0.04	0.08	-0.01	-0.13	-0.08	-0.12
	CG	**0.58**	**0.58**	0.07	0.01	0.05	**-0.25**	**0.21**
	CS	**0.69**	**0.58**	-0.08	0.10	**0.43**	-0.02	**0.39**
Channel size								
	DEP	**0.38**	**-0.34**	**0.16**	0.02	**-0.23**	-0.14	0.06
	WW	**0.81**	-0.01	-0.10	0.01	**-0.18**	-0.11	**0.13**
Fish cover								
	UNC	-0.14	0.17	0.19	-0.21	0.23	0.08	-0.11
	BED	**0.44**	**0.41**	-0.22	0.06	**0.30**	-0.11	0.16
	LWD	**-0.48**	-0.10	-0.23	0.22	-0.17	0.07	-0.07
	MAC	**-0.48**	**-0.57**	0.02	-0.15	-0.07	-0.09	0.04
	OV	**-0.53**	-0.28	0.00	0.03	-0.18	-0.01	0.08
Stream bank condition								
	RV	**-0.48**	-0.11	**0.30**	-0.19	-0.08	0.06	-0.16
	BS	**-0.42**	0.13	**0.45**	-0.05	**-0.52**	-0.12	0.11
	HM	**0.49**	0.10	**-0.57**	0.10	**0.29**	0.06	**-0.25**

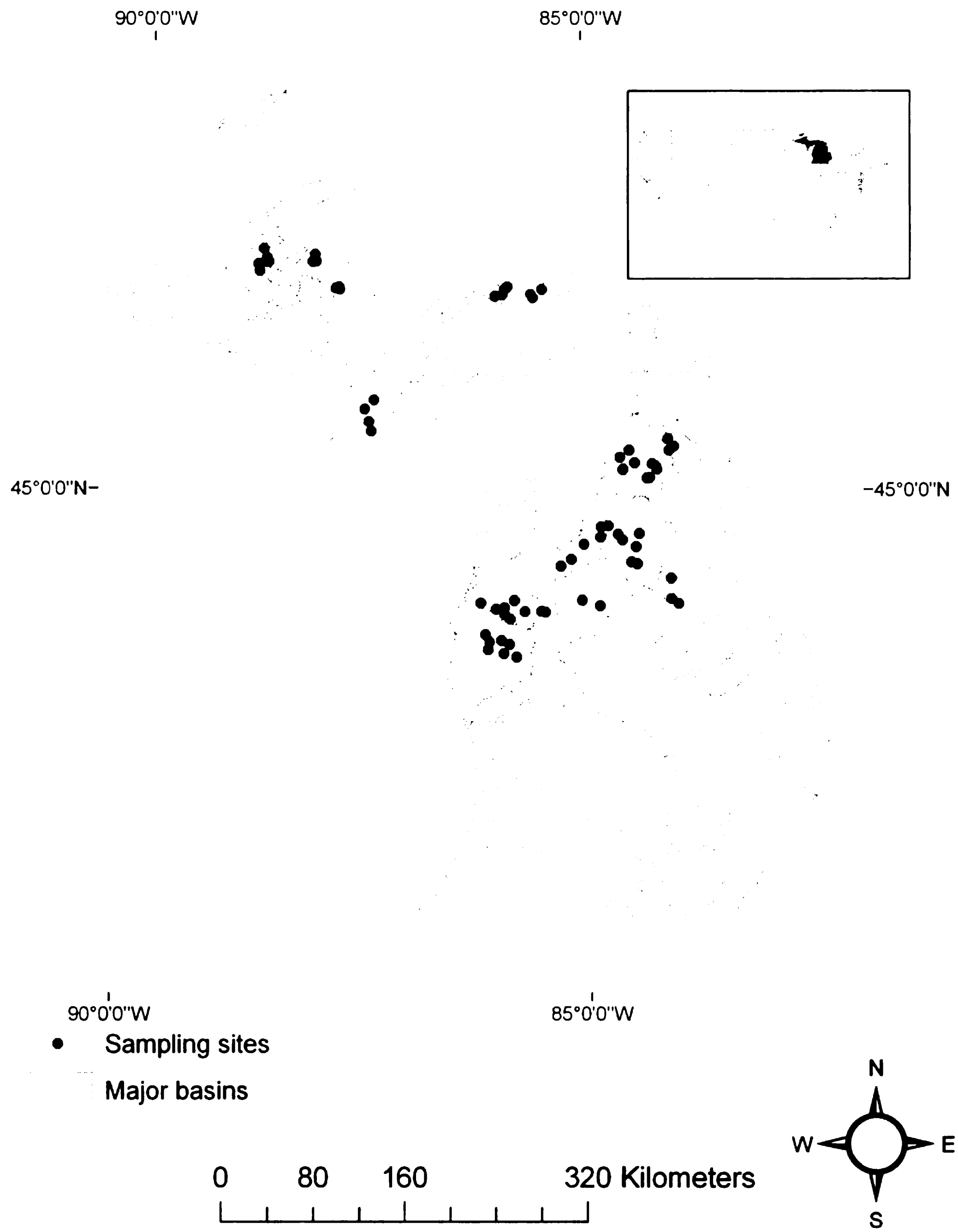


Figure 2.1: Study sites locations and major river basins in Michigan. Forty five sites were located in the Lower Peninsula and twenty were located in the Upper Peninsula.

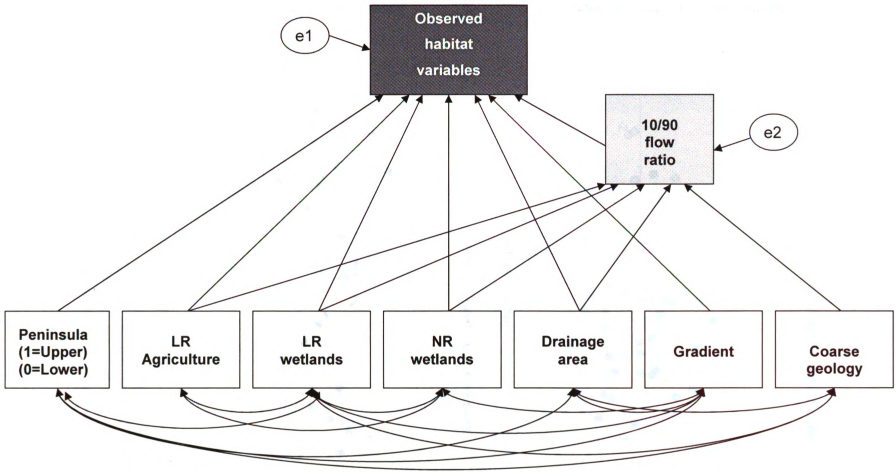
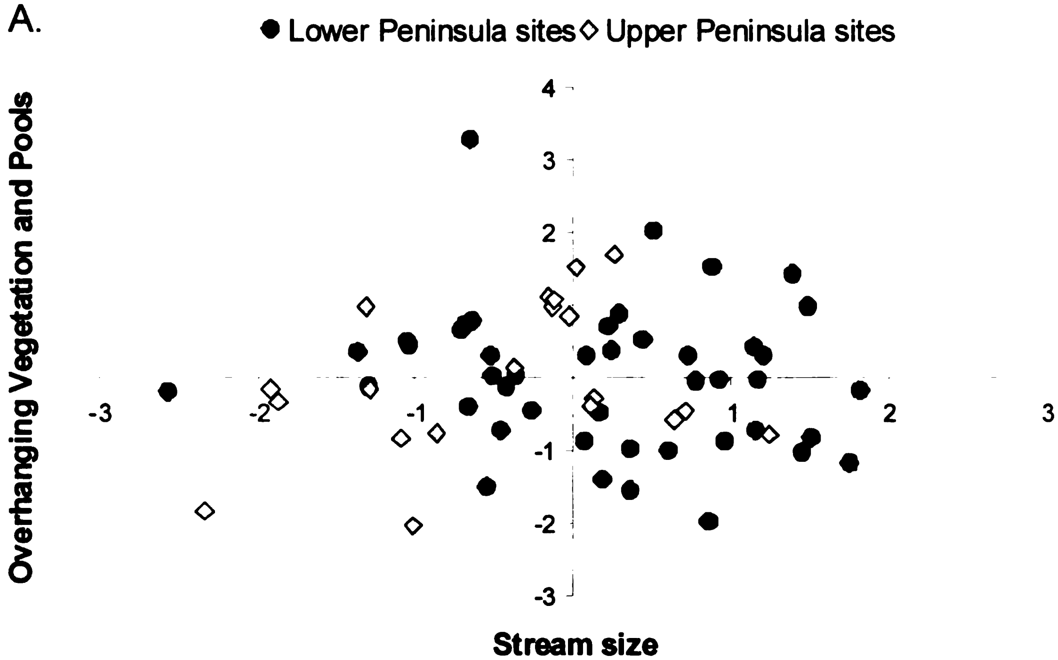


Figure 2.2: Model developed for CSA used to evaluate direct effects of landscape factors on stream habitat and indirect effects through stream flow. Error terms are included for endogenous variables and curved arrows linking landscape factors indicate correlations.

A.



B.

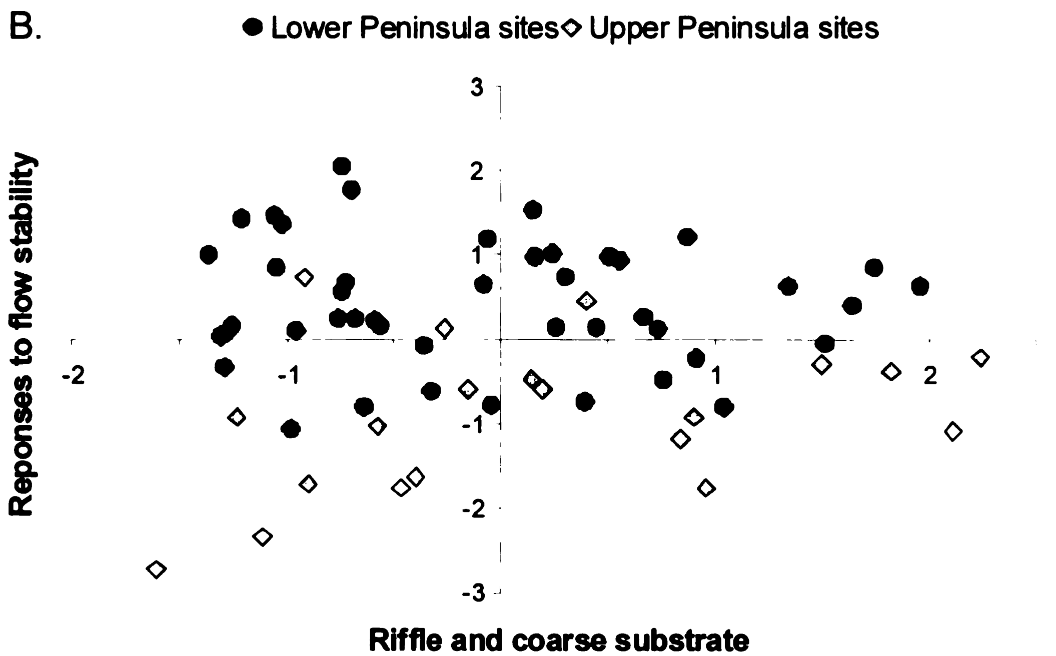


Figure 2.3: Sampling sites plotted over A. the first two axes generated by PCA of habitat variables named "Riffle and coarse substrate" and "Stream stability" respectively and B. The third and fourth axes named "Stream stability" and "Percent pools and overhanging vegetation." Note that two of the axes, responses to flow stability and stream size, show separation of study sites by peninsula.

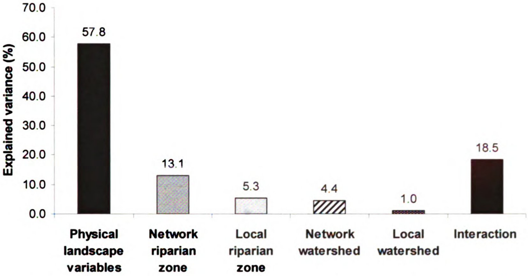


Figure 2.4: Percent of total explained variance by RDA predicting habitat variables from groups of landscape variables. A total of 41.2% of the variance within habitat variables was explained by all groups of landscape variables

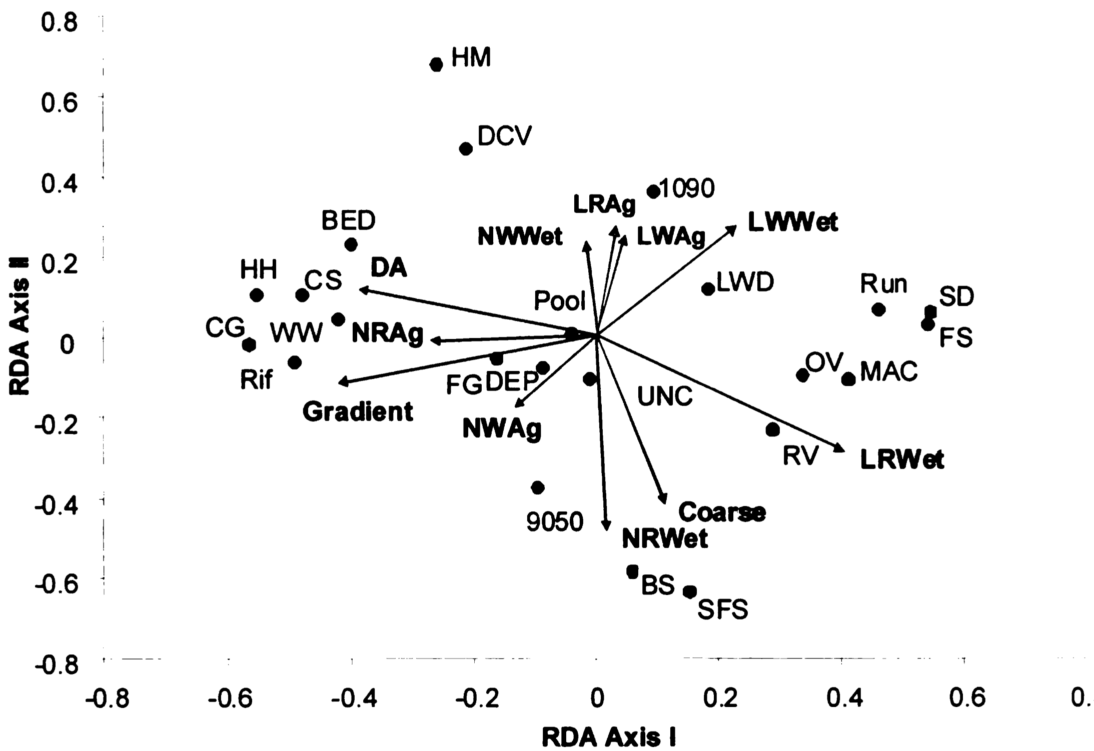


Figure 2.5: Plot of the first two axes from redundancy analysis (RDA) with vectors representing landscape features and points representing physical habitat variables. Gray text represents landscape variables while habitat variables are shown in black.

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Chapter 3

Introduction

The decline in the biodiversity of freshwater organisms globally has been described in recent assessments of imperiled organisms. Over 47% of known crayfish species within North America are now considered imperiled (Taylor et al. 1996). Mussel taxa are facing a bleaker picture within the United States and Canada, with 72% threatened (Abell et al. 2000). The number of imperiled and extinct freshwater and diadromous fish taxa in North America has increased from 363 to 700 since 1989 (Jelks et al. 2008). Salmonids alone represent 11% of listed taxa, with 46% of these being distinct populations or seasonal runs (Jelks et al. 2008).

While various factors have been cited as leading to imperilment including overfishing and the spread of invasive organisms, the degradation of habitat is considered to be a main cause of the decline of freshwater taxa, with over 71% of freshwater fish extinctions world-wide directly relatable to flow alterations, fragmentation by dams, removal of woody debris, sediment deposition, increased pollution, and sediment load (Helfman 2007). In stream systems, degraded conditions in localized reaches can further fragment suitable habitat along the longitudinal stream gradient creating unsuitable patches that constrain the movement of species and that may increase risk of species loss (Fausch et al. 2002). Habitat restoration can be used to increase the suitability of a stream system, but in some cases habitat has been altered in ways that are irreversible. In such instances, the identification of stream networks that contain ample amounts of suitable habitat may be imperative to protecting imperiled species.

The use of a Geographic Information System (GIS) is one approach that allows for the identification of potential habitat over large geographic areas. Large datasets of information on land cover, gradient, and surficial geology are available for many regions and several studies over large areas have used similar datasets to assess stream condition. At the national scale, Essleman et al. (in press) created a disturbance index based on 15 land use disturbance metrics summarized at two scales, the local catchment draining into a stream reach and the entire catchment upstream of the reach, capable of quantifying anthropogenic stress on individual stream reaches across the United States. Danz et al. (2007) summarized data on atmospheric deposition, human population, land cover, and point source pollution in order to create a regional stress index for river basins of the Great Lakes and then examined the role of stress levels on determining fish community characteristics. Such studies performed across large regions illustrate how landscape factors can be used as surrogates for stream condition, and are based on numerous studies showing specific relationships between landscape factors such as gradient, surficial geology, and land use on stream habitat conditions and quality (Roth et al. 1996, Richards et al. 1997, Wang et al. 1997, Wang et al. 2003, Infante and Allan in press).

Together, the use of landscape and in-stream habitat characteristics can be used to understand multiple scale controls on fish community composition (Tonn et al. 1990, Poff 1997, Quist et al. 2005). Tonn et al. (1990) attempted to predict community composition in lakes in two distinct geographic regions, creating a filter approach that organized different controls on fish presence at multiple spatial scales. This approach used known relationships between large scale variables and local lake conditions to predict habitat within the lake. Poff (1997) made this approach applicable to streams by suggesting the use of a hierarchical framework based in part on the spatiotemporal scale presented in Frissell et al. (1986) in which geographic, landscape, and biological filters at several spatial scales could be used to predict community composition based on characteristics needed to support specific fish species. Quist et al. (2005) used field collected data on in-stream habitat conditions to predict individual species presence or absence within a study reach. While these studies incorporate a filter approach for understanding community composition, utilizing landscape and reach scale information to predict habitat characteristics known to control a species distribution can be used to identify stream systems that a species could potentially occupy.

The Arctic grayling (*Thymallus arcticus*) is a holarctic species and in North America exists through Alaska and into Canada, extending south to Alberta and British Columbia and east into Nunavut (McAllister and Crossman 1973, Scott and Crossman 1973). The Michigan subpopulation was one of two glacial refugia subpopulations of the species within the conterminous United States, while the other is located in the upper Missouri River, Montana (Vincent 1962, Scott and Crossman 1973, Northcote 1993). The Arctic grayling was extirpated from Michigan in 1936 (Vincent 1962). A combination of habitat degradation, overfishing and competition from non-native species was believed to cause the grayling's decline and eventual disappearance (Mershon 1923, Vincent 1962, Nuhfer 1992). While several reintroductions have been attempted, none have been successful (Nufher 1992). The last reintroductions occurred from 1987 through 1991, and were attempted in a small number of lakes and rivers selected based on their remoteness of location, lack of competitor or predator species, and ability to support other trout species (Nuhfer 1992). Some individuals survived for several years in lakes but no spawning was observed, while fish stocked in rivers disappeared soon after reintroduction (within 6 months) (Nuhfer 1992). Failed reintroductions were attributed to a number of factors including lack of suitable grayling habitat, fragmentation of streams by dams, high water temperatures in some reintroduction sites, overfishing and illegal taking in open fishing areas, fungal infections, and the inability of fish to remain in the area in which they were stocked (Nuhfer 1992).

Recently, concern has been growing over dwindling subpopulations of grayling in both Alberta and British Columbia and the Big Hole River (Kaya 1992, Northcote 1993, Clarke et al. 2007, Backus 2007, Lamothe and Peterson 2007). Because of the increasing awareness of threats facing the species as well as strong local support, new research since the last Michigan reintroduction attempts has become available. Given new knowledge on habitat requirements and preferences of grayling and advances in the ability of identifying stream conditions over large areas using landscape data, the question of whether suitable Arctic grayling habitat in Michigan exists can be revisited.

My research addresses the question: does suitable grayling habitat currently exist in Michigan? To answer this question, I implemented a three-step approach to characterize stream habitat. First, for all stream reaches in my study area, I develop a hierarchical assessment tool capable of evaluating habitat suitability. Next, I rate stream segments, or connected stream reaches free of barriers to migration, based on total connectivity in the context of reach habitat suitability scores. Finally, I use in-stream data collected in the field to determine if habitat characteristics important to Arctic grayling that cannot be incorporated into my assessment tool exist in high rated stream segments. By using new data and tools to attempt to locate suitable habitat specific to a species, I plan to develop a novel approach that can be used to determine if Arctic grayling can exist within Michigan streams. My hope is that this approach will be applicable to management projects in which the goal is to determine where suitable habitat may exist for a range restricted or locally extinct species.

Methods

Study area

Historically, Arctic grayling were found in all catchments in the Lower Peninsula of Michigan north of and including the White River draining to Lake Michigan in the west and north of and including the Rifle River draining into Lake Huron in the east (Vincent 1962, Figure 3.1). In the Upper Peninsula, the species was only found in the Sturgeon River basin, in both the Otter and Sturgeon Rivers (Vincent 1962). My study area included the historic species' range in the Lower Peninsula as well as the entire Upper Peninsula. The Upper Peninsula was included because of its relative lack of human impact and because reintroductions were attempted in streams throughout this region. In general, the landscape of my study region is dominated by forests and wetlands, with small areas of agricultural and urban land uses (Wang et al. 2003, Danz et al. 2007).

A total of 69 reaches were sampled during the summer months of 2009. A reach is defined as a continuous section of surface water with similar hydrologic characteristics separated by the confluence with another reach above and below it (USGS 2004). Study reaches were selected to capture a range of landscape and land cover characteristics, to include locations with historical voucher specimens of Arctic grayling, and to include locations where recent reintroductions were attempted from 1987 to 1991 (Nuhfer 1992).

Study sites were selected within reaches based on accessibility and were located at least 1 km downstream from the first upstream confluence and at least 10 m upstream from stream entry. Site length equaled 40 times average stream width following a stream sampling protocol developed for Wisconsin by Simonson et al. (1994).

Habitat data collection and summary

Habitat data collected included measures of water depth, channel shape, bank stability, riparian vegetation type, percent overhanging vegetation, substrate type and embeddedness, percent and type of fish cover, percent of geomorphic units (run, riffle, pool), and summer water temperatures. Habitat sampling methods were based on Simonson et al. (1994). At 20 transects equally spaced throughout a sample site, five measurements were taken at regular points across each transect to characterize stream depth, dominant substrate (clay, silt, sand, fine gravel, coarse gravel, cobble, boulder, or bedrock), and embeddedness of gravel or cobble. Embeddedness was ranked in quartiles from 0-100%, with 0% indicating no or very little embeddedness, 25% indicating that individual particles of substrate are embedded to half their height, 50% indicating that substrate is heavily embedded on its sides but lacks surface cover, 75% indicating that substrate is partially covered by sediment or sand, and 100% indicating that substrate is completely covered in sediment or sand. Percent substrate types and percent fish cover type measurements including macrophytes, bedrock, boulder, and large woody debris (LWD) were visually estimated over an area 3 m on either side of the transect line. Occurrence of bank undercuts and percent of overhanging vegetation acting as cover were noted for both banks at each transect, as was the percent of riparian vegetation or land cover type within 5 m of the stream on each bank. Channel dimensions including wetted and bankfull width were measured using a rangefinder accurate to 0.5 m, while bankfull height was estimated to the nearest 0.1 m using a marked 2.5-meter segment of PVC piping. Bankfull height was measured as the difference in height between the stream flow surface at the time of sampling and the point at which water would enter the floodplain. Bank stability was visually scored for each stream bank on each transect with 4 indicating a stream bank with no visible evidence of erosion, 3 indicating some evidence of erosion and recent stream overflow, 2 showing moderate erosion causing unstable soil conditions, 1 showing heavy erosion and a deteriorating bank, and 0 indicating no structural support and maximal erosion.

To characterize habitat conditions that I was unable to measure quantitatively, I used the Michigan Department of Environmental Quality (MDEQ) Procedure 51 habitat assessment (MDEQ 2002). This method visually scores a variety of physical characteristics used to determine stream condition and habitat quality including embeddedness, variability in depth/velocity, flow stability, bottom deposition and sedimentation, geomorphic unit diversity, bank stability, bank vegetation stability, and streamside cover. July temperatures were recorded at 27 of the 69 sites using Hoboware Pro temperature loggers. Temperature loggers were placed in streams throughout the month of June and collected in August. Mean daily temperature was calculated for each reach for the month of July.

Landscape and modeled reach data

The stream coverage used in this analysis was the National Hydrography Dataset (NHD) defined at a 1:100,000 scale (USGS 2004a). Drainage area was calculated using reach catchments delineated from the NHD and National Elevation Dataset (NED, USGS

2004b). Landscape data used in this study were organized at two different spatial scales for each stream reach: the network catchment and the network riparian zone. Network refers to the area upstream of the reach throughout the watershed or riparian zone. The riparian zone is classified as a 60 meter region on either side of the stream. Data on land cover (IFMAP 2001) and surficial geology (Farrand and Bell 1982) were summarized, with percent forest and percent coarse geology summarized at the network catchment scale, while percent urban, agriculture, and open and forested wetlands summarized at the network riparian zone scale. Coarse geology is known to influence stream stability and stream temperature (Seelbach and Wiley 1997, Seelbach et al. 2007) and is the percent of geologic types with high hydraulic conductivity (values greater than 5.0 m/d), which describes the relative velocity at which water moves through porous spaces in soil (Shepherd 1989). Stream gradient summarized at the reach scale was the drop in meters per meters of stream reach as depicted by the NHD coverage. See Brenden et al. (2006) for further explanation of catchment delineation.

Stream flow regimes were characterized for each stream reach using a model of groundwater delivery to stream channels, precipitation data, surficial geology and land use (Seelbach et al 2007). The 10/90 ratio, the annual flow that is exceeded 10% of the time divided by the annual flow exceeded 90% of the time, was calculated and used as a metric for estimating stream flow stability. A 90/50 ratio, the annual flow exceeded 90% of the time divided by the annual flow exceeded 50% of the time, was calculated to indicate areas with high baseflow (Raleigh 1982). Modeled July mean stream temperatures were predicted using statistical models based on relationships of sample temperature measurements and landscape data from throughout Michigan (Werhly et al.

2009). The majority of observed July mean temperatures (89%) were lower than the modeled temperatures used in my assessment tool and close to observed values, with a 4.6° C maximum deviation from the observed value (Figure 3.2). Only three of twenty-seven sites had higher temperatures than predicted, all within one degree of their modeled temperature. Given these results, I felt that using modeled temperatures within my assessment was justifiable.

Fish data and index of biotic integrity

Brook trout abundance and fish assemblage data were from the Michigan Department of Natural Resources (MDNR) Fish Collection System and Michigan Rivers Inventory databases (Seelbach and Wiley 1997). These collections were made largely through backpack or barge electrofishing, and samples that were collected using rotenone were corrected using information from sites that contained both electrofishing and rotenone samples (Seelbach et al. 1994). Fish were identified and counted in the field.

Wang et al. (in press) calculated index of biotic integrity (IBI) scores for coldwater stream sites using the Wisconsin coldwater IBI procedure (Lyons et al. 1996), while wadeable warmwater IBI scores were calculated using methods outlined in Procedure 51 (MDEQ 2002) then adjusted for ecoregion differences (Wang et al. 2008). Both coldwater and warmwater IBI scores were calculated for marginal (coolwater) trout streams and the high of the two values was used to represent a stream reach, because no coolwater IBI for the region currently exists (Wang et al. in press). IBI scores scaled from 0 to 100, with 90-100 being deemed excellent, 60-80 good, 30-50 fair, 10-20 poor, and 0-10 being very poor (Lyons et al.1996).

Overview of the assessment tool

The tool developed to assess habitat suitability incorporated a series of hierarchical filters that accounted for stream habitat conditions important to Arctic grayling. Filters included natural catchment landscape variables, land cover at the network catchment and network riparian zone scales, and modeled variables specifically describing conditions in stream reaches (stream flow and temperature). The method follows approaches and ideas of Tonn (1990), Poff (1997) and Quist et al. (2005), who use hierarchical filters to predict fish assemblages in lake and river systems using geographic (historical species distribution and separation due to physical barriers), landscape, and biotic variables. My use of the filter approach did not focus on predicting fish distributions directly, but instead was used to rate streams based on their suitability of habitat characteristics for Arctic grayling. These filters were organized over three spatial scales; the network catchment, the network riparian zone, and the reach. My framework contained five hierarchical filters: drainage area; network catchment conditions, network riparian conditions, reach conditions; and stream temperature (Figure 3.3). Once an individual reach score was determined, the length of a stream between barriers to migration, i.e., the total connectivity of a stream segment, was calculated. A "habitat-weighted connectivity" score was then applied to each reach, a measurement created to address the concept that fish migration length is dependent on the quantity and quality of habitat within a connected stream segment (Benke 1992, Fausch et al. 2002). Habitat-weighted connectivity scores were then summarized and weighted by total length within a stream segment to create a final stream segment rating.

In order to determine breaks in suitability of landscape drivers, I graphed relationships between landscape conditions and potential response variables. The frequently non-linear relationships of habitat and biological characteristics with landscape features have been used to mark theoretical thresholds indicative of ecosystem condition or health (Huggett 2005). In this study, I defined a threshold as a zone rather than a point, indicative of a gradual shift from one ecological state to another (Marudian 2001, Huggett 2005). The zones above and below this range would then represent differing ecological states. Monitoring disturbance variables in an attempt to keep conditions from reaching a point where degradation may be irreversible is one application of thresholds (Wiens et al. 2002). However, I used threshold zones in a different way, to examine changes in relationships between landscape factors and variables indicative of stream quality and condition potentially important to Arctic grayling. Specifically, I used fish IBI scores, 10/90 ratio, and a visual metric of stream flow stability as response variables. I believed that for values within the suitable range determined for a predictor variable, it was more likely that the specific reach would have characteristics suitable for grayling. The marginal range would be less likely to have suitable habitat, while the poor range would be the most likely to have conditions unsuitable for grayling.

Scoring stream reaches

Predictor variables were assigned a suitability score ranging from 0 to 2 (Table 3.1), with breaks defined by conditions known to support Arctic grayling, habitat responses to landscape characteristics, or thresholds identified to depict variable responses to large-scale controls (Table 3.2). Depending on the cumulative value of variables at each filter, a stream reach was then assigned a score ranging from 1 to 2 or 0 to 2, and the sum of all filter scores was considered the individual reach score. I chose to include a score of "0" for reach scale and temperature filters because of the limiting effects of variables relating to flow stability, depth for cover, gradient, and temperature on Arctic grayling survival. At the network catchment and network riparian zone, high human disturbance and low coarse geology are indicative of conditions unsuitable for Arctic grayling, but the response of stream health metrics to these large-scale variables can be affected by other factors and may vary in their response across reaches despite general trends. Therefore, I felt it would be inappropriate to apply a score of zero or consider a stream unsuitable because of a single landscape feature. The reach scale variables had a more direct effect on the physical habitat available to the Arctic grayling, and therefore the cumulative total score of 10/90 ratio, 90/50 ratio, and gradient was re-scored 0 to 2, with 0 indicating that the reach was most likely unsuitable for sustaining a population. Temperature was treated as its own filter due to the importance of stream temperatures to salmonids (Brett 1979, Richter and Kolmes 2005) and zero values were given to sites above 20°C. I believe that of all the variables I examined temperature was the only one that could reasonably exclude grayling existence within a stream reach, and therefore treated an unsuitable temperature score (0) as multiplicative.

Rating of stream segments

Due to the Arctic grayling's tendency to migrate long distance between spawning, overwintering and feeding sites (West 1992, Lamothe and Mage 2003), I attempted to account for habitat-weighted connectivity among stream reaches of various rankings within my assessment tool. Locations of dams were determined using a dam layer created by the Michigan Department of Environmental Quality in 2000, with locations corrected by the Institute for Fisheries Research at Ann Arbor in 2004. I used a Michigan atlas, aerial photography, information on individual dams within the dataset, and Google

Earth to estimate the position of each dam on the NHD stream layer. Dams that occurred on reaches not included in the NHD stream layer were deleted, while all others were manually linked to the stream layer. A data layer consisting of points representing inflows into the Great Lakes was joined with the dam layer. The NHD stream layer was transformed into a network dataset, and the network analyst tool within GIS was used to estimate the distances between barriers in stream systems. Barriers could be dams, Great Lakes, or large natural inland lakes in lower reaches of a system.

Reaches were then re-rated based on the total length of the stream segment in which it occurred (Figure 3.4). Because Arctic grayling are known to migrate long distances (40-50 km) but are not likely to travel to each reach summarized in the stream segment (West 1992, Lamothe and Magee 2003), I used a break value double that of expected migration length to define streams with ample connectivity (100 km). The shortest known area to contain a fluvial Arctic grayling population is just less than 6 km, but exists in a unique and highly modified canal (Barndt and Kaya 2000). Therefore, I used 10 km as a lower break for scoring between marginal and unsuitable connectivity. Reaches located within stream segments with a length of greater than 100 km kept their previous score of 0 to 2 (Table 3.3). Reaches with segment lengths between 10 and 100 km were dropped one score (2 dropped to 1 and 1 dropped 0), while all reaches with a segment length less than 10 were given a scored a 0. Reach scores were then weighted by their individual length, which were then summarized as a total value across the stream segment divided by the total length of the stream segment in order to create a final stream segment rating between 0 and 2.

Identification of in-stream habitat and validation of assessment tool

Segments were summarized by their final rating into top (1.50-1.70), high (1.30-1.49), marginal (1.10-1.29), low (0.90-1.09), and lowest (0.00-0.89) groupings. Individual variables included within filters were then compared across segment groups to examine trends in variable scores as segment rating increased. Average total scores for the visual habitat assessment protocol were also compared to final stream segments groupings.

Additional in-stream data collected from study sites were summarized to identify if habitat characteristics important to Arctic grayling survival but not included in my assessment tool were present in high rated stream segments. Characteristics included percent and type of gravel in riffles for spawning and presence of deep, stable pools and runs for summer feeding habitat. Presence of various game fish species were also summarized. For high rated stream segments within my study region I also considered the occurrence of potential predators and competitors of Arctic grayling in these streams.

Results

Landscape conditions

Drainage area of my study reaches ranged from less than 1 to 10,373 km^2 (Table 3.4). Forest land cover in reach catchments had a mean value of 60%, and coarse geology was dominant, with a mean value of 71%. Reach network riparian zones had relatively low levels of human land uses; percent agriculture's mean value was 6% while urban land use was low with a mean of 2%. Wetlands were common in network riparian zones, with a mean value of 37%. Reach gradient varied by two orders of magnitude, from 0. 01% to 1.78% across study reaches, and 10/90 flow ratio varied from as low as

1.1 to 640.9, with a mean of 16.3. July mean temperatures were low overall, with an average of 16.4°C.

Break points of variables included in the habitat scoring system

Reaches with a drainage area between 40 km^2 and 620 km^2 were deemed most suitable for the Arctic grayling and given a score of 2, while all others were given a score of 1. The break in suitability for small drainages was determined by multiple factors. First, grayling were known to historically inhabit medium to large streams in Michigan (Vincent 1962) and therefore smaller drainage areas may be indicative of less suitable habitat. Also, when brook trout abundance was plotted against drainage area (Figure 3.4), high abundances of brook trout occurred in small drainage areas. Given this information, I concluded that grayling are more suited for larger streams, and in smaller streams, brook trout are a potential competitor. The break between the suitable zone and the marginal threshold zone was set at the point at which brook trout abundance decreased, 40 km^2, which was also the upper end of "small" sites as defined by the Michigan Department of Natural Resources (MDNR) Status and Trends Sampling protocol. The break in suitability for larger drainages was determined to be 620 km^2, the "very large" distinction in the Status and Trends Sampling protocol (Wills et al. 2008), and was chosen because grayling may be limited by predation in these bodies of water (Vincent 1962).

Percent coarse geology and forest land cover were both included in the network catchment condition filter. Reaches with less than 50% coarse geology scored a 0, reaches with 50% to 80% scored a 1, and reaches with greater than 80% scored a 2. These breaks were determined by plotting the 10/90 flow ratio against coarse geology

(Figure 3.5). Sites with greater than 50% coarse geology have a notable decline in the lower limit of 10/90 ratios, indicating increasing stability. This trend continues until approximately 80% where a higher density of low values can be found and the lower limit stabilizes at about 2. Suitability of forest cover in the network catchment was also broken into three groups; reaches with greater than 60% forest in the network catchment scored a 2, 30-60% a 1, and less than 30% a 0. These breaks were determined by plotting fish IBI scores against percent forest land cover to determine points at which biological integrity changed (Figure 3.6). IBI scores for fishes are commonly used to indicate the "health" of a stream and can be useful when considering effects of land use disturbance (Fausch et al. 1990). Above approximately 30% forest land cover, the number of low IBI scores decreases and continues to decrease until 60% forest land cover, after which no IBI values below 40 exist. Total scores for percent forest and coarse geology cumulatively ranged from 0 to 4, with 0 to 2 being ranked a 1 and 3 to 4 being ranked a 2 for the network catchment scale.

Percent urban, agriculture, and wetlands land cover were assessed within the network riparian landscape condition filter. Reaches with percent urban land cover less than 5% were scored a 2, 5-15% a 1 and greater than 15% a 0. Fish IBI scores from Michigan were plotted against percent urban in the network riparian zone to determine thresholds in biological integrity (Figure 3.7). No sites with greater than 5% urban land cover were ranked as "excellent" in terms of their IBI scores; therefore, I determined that sites with less than 5% urban land use have the most likelihood of exhibiting high biological integrity. In contrast, sites with greater than 15% urban land use had IBI scores that were almost entirely ranked "fair" or "poor," and I used that to determine a point above which sites would be least suitable for grayling. Reaches with agriculture land use less than 10% were scored a 2, 10-40% a 1, and greater than 40% a 0. Fish IBI scores were also plotted against percent agricultural land use in network riparian zone to determine breaks in suitability (Figure 3.8). Above 10% agriculture, a general trend in decreasing "good" scores was observed, with increasing "fair" and "poor" scores and a sharp drop-off in scores overall at 40% agriculture in the network riparian zones. The visual estimate of stream flow stability was plotted against percent wetlands in the network riparian zone (Figure 3.9). Reaches with greater than 25% wetlands were scored a 2, while those with less than 25% wetlands were scored a 1. Reaches with more than 25% wetlands in the network riparian zone were found to have a maximum score of 10 (the highest possible) and a minimum of 4, while those with less 25% had a maximum score of 7 and a minimum score of 2; consequently, I set breaks in suitability scores to reflect these trends. Cumulative scores for urban, wetlands and agriculture in the network riparian zone were 0 to 6, with values of 0 to 3 being given an overall network riparian score of 1 and values from 4 to 6 given an overall score of 2.

Stream gradient, 10/90 ratio, and 90/50 ratio were assessed within the reach condition filter. Stream gradient values from 0.09% to 0.30% were given a score of 2, 0.31% to 1% given a score of 1, and values less than 0.09% or greater than 1% were scored 0. Stream gradient breaks were determined based on historical accounts of Arctic grayling, which described gradient for optimal environments ranging from 0.09% to 0.29% in Michigan (Vincent 1962) and 0.28% in Montana (Liknes and Gould 1987). While Vincent (1962) describes a maximum gradient of 0.38% for Arctic grayling, I chose a higher value of 1% because brook trout and grayling in the Upper Big Hole River showed low interspecific competition in areas with less than 1% gradient (Byroth and Magee 1998). Ten-ninety ratios above 20 were given a score of 0, 10 to 20 a 1, and below 10 a 2. Fish IBI scores were plotted against 10/90 ratio across Michigan to assess thresholds in biological integrity associated with stream stability (Figure 3.10). At a 10/90 ratio of 20, IBI scores show a sharp decrease in general, and "excellent" scores do not occur after this point. I considered values greater than 20 to be unsuitable in the rating system. Because of the importance of stable flow to the survival of Arctic grayling (Vincent 1962, Kreuger 1981, Liknes and Gould 1981, Lamothe and Magee 2004), I chose to create a second break at a 10/90 ratio of 10, differentiating between streams stable enough to support most fish species and streams that could be considered extremely stable. Reaches with 90/50 ratios greater than 0.55 scored a 2, 0.25 to 0.55 a 1, and less than 0.25 scored a 0. Ninety-fifty ratio was considered a surrogate for depth and baseflow (Raleigh 1982, Raleigh et al. 1986), and breaks in 90/50 ratio within the habitat suitability index model for brown trout, *Salmo trutta*, were used in my assessment (Raleigh et al. 1986). I believe that given the importance of depth as cover to both brown trout and grayling and in the absence of information specific to grayling, that 90/50 ratio breaks used to identify brown trout habitat can be applied to Arctic grayling as well (Raleigh et al. 1986, Byroth and Magee 1998). Stream gradient, 10/90 ratio and 90/50 ratio have a cumulative possible score of 0 to 6 at the reach scale. This cumulative score was then rescored for the filter, with 0 to 2 being scored a 0, 3-4 scored a 1, and 5-6 scored a 2.

Suitability of July mean temperature was based on known estimates of critical and optimal temperatures for growth in different regions for the Arctic grayling. Streams with

July mean temperature less than 16 °C were scored a 2, 16-20 °C a 1, and greater than 20 °C a 0. Because I was using modeled mean temperatures, I chose a value less than described critical maximum values for Montana populations (23 -25 °C) (Lohr et al. 1996, Lamothe and Peterson 2007) as the break between marginal and unsuitable river systems, while high rates of growth were shown to occur between 7.5° and 16 °C (Hubert et al. 1985).

Overall, land cover and landscape characteristics were suitable for many the reaches in the study area, with a majority at each filter, 60.12% at the network catchment and 85.04% at the network riparian zone, receiving rankings of 2 (Figure 3.11). Drainage area and variables at the reach scale acted as more discriminating filters. Drainage area had only 21.55% of reaches score 2, while the reach habitat filter had 44.35% scored as 2, 49.49% as 1, and 33.57% as 0. Nearly 10% of streams scored a 0 for July mean temperature, while 44.35% of streams were considered suitable and received a score of 2.

Scored stream reaches

Overall individual reach scores ranged from 0 to 10 before connectivity was applied. High scoring reaches (cumulative score greater than 8) made up 9.3% of the total reaches in Michigan and were located in the northern portion of the Lower Peninsula (a total of 13.4% of Lower Peninsula reaches) (Figure 3.12). In the Upper Peninsula, high rated reaches were less common (6.2% of Upper Peninsula reaches), with the majority existing within the central portion just west of Munising as well as a small amount in the west. The majority of reaches scored 5 to 8 in my assessment tool (78.8%).

Rated stream segments

Segments were summarized by their final rating into top (1.50-1.70), high (1.30-1.49), marginal (1.10-1.29), low (0.90-1.09), and lowest (0.00-0.89) groupings. After incorporating connectivity across stream reaches, final stream segment rating ranged from 0.00 to 1.70 (Figure 3.13). The top rated segment was the Little Manistee River (1.70) in the Manistee watershed (Table 3.5). Five of the six remaining high-rating segments also occurred in the Lower Peninsula: the Pine, Sturgeon, Pere Marquette, Upper White and Upper Au Sable Rivers (Figure 3.14, Table 3.5). All of these Lower Peninsula streams had historical records of grayling being present, supported by voucher specimens or written accounts (Unknown 1879, Mershon 1923, Bailey et al. 2006). The Sucker River was the highest rated Upper Peninsula river (1.38), located east of Munising and flowing into Lake Superior. The majority of marginal stream segments occur in the Lower Peninsula (63.6%), with the other four occurring in the central and western Upper Peninsula. Segment scores in which reintroductions were attempted ranged from 0.00 (Section 34, Spray Creek) to 1.21 (Upper Manistee), with an average score of 0.63. Reaches in Spray and Section 34 Creeks had marginal rankings before connectivity was applied, but ranked lower after due to their relatively short lengths.

Evaluation of grouped stream segments

Stream segment groups plotted against individual predictor variables had increasing suitability scores as rating increased. Overall, network watershed and riparian zone land cover characteristics for high rated and top rated segments fell within the range considered suitable for Arctic grayling (Figures 3.15-3.18). July mean temperature scores for all segment groupings had mean values close to the suitable range (Figure 3.19). Percent coarse geology and reach specific variables (gradient, 10/90 ratio, and

90/50 ratio) increased across groups of sites with higher ratings (Figures 3.20-3.23). Segments that rated marginal or low in the assessment also showed greater variability in individual variables scores than the high or top segment groupings.

Stream segments in which reintroductions were attempted had land use, land cover, and July mean temperature scores that fell within the suitable range. Average scores of reach scale variables ranked lower for reintroduction sites than for high and top stream segment groupings, and were more variable. Reintroduction segments had a wide range in percent coarse geology, from 0 to 90%, with the mean value falling within the unsuitable range. Reintroduction segments also had mean gradients within the unsuitable range (>0.01) and the lowest average 90/50 ratio of all groups.

Total score for the visual habitat assessment protocol showed an increasing trend with segment score, however marginal, low, and lowest grouped segments were very similar in mean and distribution of scores (Figure 3.24). Total scores greater than 154 are considered excellent, 105-154 are considered good, 56-104 are classified as marginal, and less than 56 are classified as poor (MDEQ 2002). Sites within top ranked segments had a mean value on the high end of good (138) with some values ranging into excellent. Visual assessment scores at reintroduction sites (Upper Manistee River, Mulligan Creek, and the Huron River) ranged from marginal to good, with a mean value of 102, the lowest of all groups.

Identification of in-stream habitat critical to Arctic grayling life history characteristics

Geomorphic unit composition in the top rated segments was dominated by runs, with some pools and riffles present (Table 3.6). On average, pools comprised less than 10% of reaches within top rated segments with the Little Manistee (7.4%), the Pere

Marquette (6.0%), and the Pine (5.9%) having the most. Riffle habitat varied from 2.19% throughout reaches in the Pere Marquette to as high as 40.7% in the Sturgeon River.

Riffle substrate composition varied across high rated streams, ranging from clay to boulder (Table 3.7). Four out of six streams were dominated by fine or coarse gravel (cumulative totals greater than 50.0%), while the Sucker River had 40.18% gravel and the Pine had 19.2%. Fine gravel was present in all streams, ranging from 1.04% for the Sturgeon River to 30.0% for the Pere Marquette River. Average embeddedness was less than or equal to 50% in most streams, while fine gravel in the Sucker and Pere Marquette Rivers had higher embeddedness of 70.8% and 75.0%, respectively.

Pools within stream segments had overhanging vegetation present over 30% of the time (Table 3.8). Average in-stream pool cover was less than 35% in all pools, with the highest percent cover in the Sucker River (33%). Banks were largely stable, with mean value greater than 3. Average pool depth was greater than 0.6 m in all segments except the Pine and Sturgeon River, while the Sucker River in general had the deepest sampled pools (mean of 0.80 m).

Runs in top rated segments all had average depths greater than 0.40 m (Table 3.9). Bank stability was good, with averages close to or above 3 in all segments. Mean in-stream cover was less than 30% over all segments, with the Sucker River having the most (28.6%).

Presence/absence of other species

All stream segments within high or top ranked groupings have game species present based on MDNR sampling records that could be potential predators or competitors of Arctic grayling. Brook trout and brown trout were present in every stream segment (Table 3.10), while rainbow trout, *Oncorhynchus mykiss,* were present in every segment except the Upper White River. Salmon, *Salmo spp.,* are found in the Sucker, Pere Marquette, and Little Manistee Rivers, while steelhead were also recorded in the Little Manistee. The Pere Marquette and Pine River also support large non-salmonid species including northern pike (*Esox lucius*) and largemouth bass (*micropterus salmoides)* that may act as predators.

Discussion

Overview

By creating an assessment tool capable of integrating environmental factors across multiple spatial scales, I was able to score northern Michigan streams based on their potential ability to support the Arctic grayling. My assessment tool provided a hierarchical framework for understanding the influence of landscape on habitat suitability specific to the Arctic grayling. My results showed that characteristics summarized across large (network catchment) and intermediate (network riparian zone) scales were suitable over a wide range of my study region, while reach-specific variables (90/50 ratio, 10/90 ratio, stream gradient) and drainage area were limiting in determining a segments suitability. In addition, a measure combining a habitat score for stream reaches with a score for unfragmented lengths of stream segments in which reaches are located was developed to indicate whether long migration paths containing high quality habitats were available. This allowed us to create a final rating applied to all stream reaches throughout northern Michigan that described the habitat-weighted connectivity of a stream segment. My results suggest that there are stream segments within Michigan that have physical habitat conditions suitable of supporting Arctic grayling, including the Little Manistee, the Upper White and others in the Lower Peninsula and the Sucker River in the Upper Peninsula. However, biological interactions with other fish species could be a limiting factor and should be considered.

Habitat assessment

Habitat assessment occurred in two steps: application of a hierarchical filter approach over multiple spatial scales and an assessment of habitat-weighted connectivity. The first step followed a landscape approach in which I considered the stream in the context of surrounding and upstream landscape conditions at multiple spatial scales (Wiens 2002) as well as incorporating modeled flow and temperature at the reach scale. Modeled after the works of Tonn (1990), Poff (1997) and Quist et al. (2005), I used hierarchical filters over several spatial scales to determine the suitability for a fish species based on known and theorized responses to habitat characteristics. Tonn (1990) first proposed that historical factors and geographical location were major controls on fish assemblage in lakes with individual characteristics acting as filters to constrain the types of species that a given lake could support, a theory later incorporated by Poff (1997) and applied by Quist et al. (2005) in stream systems. While Poff (1997) focused on large-scale predictors of fish assemblage in stream systems, Quist et al. (2005) used elevation and reach-scale data such as stream width, depth, presence of LWD and geomorphic unit composition to predict fish assemblages. While applying the same conceptual filtering approach developed by Tonn et al. (1990), Poff (1997), and Quist et al. (2005), my approach in assessing stream reaches differed in both the overall goal and methodology. First, I did not attempt to predict a fish assemblage that already existed (Tonn et al. 1990, Quist et al. 2005), or focus on the presence of functional groups of fishes (Poff 1997). Instead, I focused on identifying the most suitable habitat for a species. Another difference was that while the methods above incorporated the removal of stream fish at each filter to determine which were mostly likely to occur in a particular stream, I allowed all reaches to be considered at all scales, then implemented a final rating for each. This was because I believed that reach scale factors could actually limit but not necessarily exclude the existence of Arctic grayling within a segment. Finally, my reach assessment also attempted to incorporate both landscape scale data to broadly capture habitat characteristics and modeled information specific to stream reaches.

The second step in the application of the assessment tool was to consider the habitat-weighted connectivity of individual stream reaches. Fausch et al. (2002) notes that understanding the interactions with the landscape and habitat suitability across the entire river system in which a species is found is important for developing effective reintroduction strategies. Fausch et al. (2002) defines this spatial unit of the stream system and the landscape around it the "riverscape," a unit that I attempt to incorporate into my investigation. While Arctic grayling are known to migrate long distances, it can be assumed that the length of annual migration is in part a response to availability of habitat within the segment through which it migrates (Benke 1992, Fausch et al. 2002). Because of this, after the application of the habitat suitability rating to stream reaches, I re-scored stream reaches individually based on their total connected length within a segment. By making the score dependent on the previous habitat score and total distance, I developed the habitat-weighted connectivity score. Then, by rating stream segments based on the length of each functional connectivity score (0,1 or 2) within it, I attempted to establish that the context of the individual reach within a segment matters, following from the concept of the riverscape (Fausch et al. 2002) and landscape ecology concept that patch context matters (Wiens 2002).

High rated stream reaches versus former reintroduction locations

My results show that the Little Manistee, Pine, Sturgeon, Upper White, Upper Au Sable and Pere Marquette Rivers in the Lower Peninsula and the Sucker River in the Upper Peninsula may offer the best chance for Arctic grayling survival based on their habitat characteristics. The Little Manistee was the top-rated system, with both reach characteristics and connectivity that suggest slow stable flows, cold stable temperatures, relatively deep water for cover, and high water quality due to limited human impact. Greater variability in specific variable scores below these high rated segments indicates that stream segments rating marginal and lower tended to have one or more variables that were unsuitable. Further, the lower mean value for the total Procedure 51 score for marginal vs. high rated segments indicates that marginal streams have lower habitat quality in general.

Segments that included reintroduction sites had a mean rating that fell within the lowest group of stream segments. Scores for three of the reintroduction sites (Spray Creek, Section 34, and the Cedar River) were lowered significantly due to low connectivity. The Upper Manistee River was the only site that historically supported the Arctic grayling that has not had severe alteration due to impoundments. It was the highest rated segment with a reintroduction attempt but fell within the segment group that I classified as marginal. The Middle Au Sable River was also know to historically contain Arctic grayling, but now has the Mio Dam as its upper boundary and the Alcona Dam impoundment as its lower. Because of their overall low mean rating, I believe that sites chosen for past reintroductions may not have been the most suitable. Again, reintroduction locations were largely selected based on remoteness of location, the ability to support trout, and lack of predator species, and it was concluded that reintroduction failures may have been due to lack of suitable grayling habitat, fragmentation of streams by dams, and high water temperatures (Nuhfer 1992). Reach specific variables including gradient, 10/90 ratio, and 90/50 ratio were the limiting variables – those that lowered the reach scores – within reintroduction segments. Reintroduction locations also had wide variation in amounts of coarse geology in their catchments, which can lead to stable flows and higher baseflows in Michigan river systems (Seelbach and Wiley 1997, Seelbach et al 2007). Large amounts of forest in their network catchments as well as low urban and agricultural land use in the network riparian zone of reintroduction streams indicate that disturbances resulting from anthropogenic land uses probably did not play a role in limiting reintroduction success.

In-stream habitat of high rated segments

My assessment tool focuses on identifying stream segments most likely to have habitat conditions capable of supporting Arctic grayling based on landscape factors and modeled estimates of stream habitat data. However, in-stream habitat data collected from a subset of sites allows us to validate the results of the assessment tool and also consider specific characteristics that I was unable to account for but are known to be important to grayling. These characteristics include presence of stable pools important for overwintering, deep, stable runs important for feeding, and the presence of riffles and gravel substrate important for reproduction.

Suitable stream geomorphic unit composition for Arctic grayling includes an abundance of deep, slow runs with pools for overwintering and riffle habitat for spawning (Vincent 1962, Hubert et al. 1985, Lamothe and Peterson 2004). Through the Big Hole River, Montana, reaches were quantified as 66% runs, 20% pools and 14% riffle habitat (Lamothe and Peterson 2004). The same study showed that pools greater than 0.60 m in depth having stable banks and high percentages of overhanging vegetation had high numbers of grayling (Lamothe and Peterson 2004). While little information is given specific to historical condition in Michigan, grayling were known to occupy runs of most large rivers in my study region, suggesting that they may have used runs to feed, making depth and stability important within runs (Mershon 1923, Vincent 1962).

Areas suitable for spawning are riffles with substrate dominated by gravel, with fine gravel being more present than coarse, and limited amounts of fine sediments (clay, silt, sand) and coarse substrate (cobble, boulder, bedrock) (Liknes 1890, Vincent 1962, Tack 1971, Tack 1973, Butcher et al. 1981, Hubert et al. 1985, Shepard and Oswald 1989). Grayling eggs tend to adhere to fine gravel, making gravel size an important factor for spawning success (Tack 1971, Tack 1973).

Overall, the Little Manistee River is the most suitable for Arctic grayling based on the landscape assessment tool and in-stream habitat characteristics selected from a subset of sites. Its deep, stable runs and pools combined with limited sediment load and gravel-dominated riffles would theoretically support many of the life history needs of the species.

Most of the top ranked streams had stable banks, deep runs and pools for cover and ranked highly using the Procedure 51 visual habitat assessment protocol. The limited amount of cover in most streams, with the Sucker River being an exception, is not a concern for their ability to support Arctic grayling, given that adults occupy streams with limited in-stream cover successfully, using depth instead of LWD, rock cover, or macrophytes (Byroth and Magee 1998). The Pere Marquette and Upper Au Sable Rivers, although scored as suitable, had higher levels of fine sediment and embeddedness than other systems and are not ideal for spawning. The Sucker River may be limited due to high levels of embeddedness within spawning sites as well (Raleigh 1982, Byroth and Magee 1998,). The Pine and Sturgeon Rivers may have riffle substrate that is larger than ideal for grayling spawning, while the presence of riffles with large substrate and low percentage of runs in both streams indicates a swifter flow, potentially less suitable for a species that prefers high velocity locations of the stream (Byroth and Magee 1998).

Consideration of biological factors

While suitable physical habitat seems to be present in several stream segments within Michigan, the presence of species that could potentially act as competitors or predators is a concern if reintroductions were considered. In all of the top-rated stream segments, brook trout, brown trout and rainbow trout are present, and at least one of the streams, the Little Manistee, supports steelhead. Although competition from brook trout may not be a factor in larger streams where depth is used as cover, competition with brown trout could be. Brown trout are known to occupy similar areas of the stream as grayling, using depth as cover and feeding heavily on stream drift (Raleigh et al. 1986). Rainbow and brown trout are also know to feed on other fish, and in many of the top-ranked stream segments both of these species are known to reach large sizes, potentially feeding on grayling, limiting the success of fry and juveniles. Although I am not aware of any research on the effects of these two species on the Arctic grayling, it is hypothesized that one factor in the restriction of populations to the extreme upper Missouri was initially caused by the movement of rainbow and brown trout into lower reaches, but constrained by limited suitability for these two species in the upper reaches (Kaya 1992, Campton 2006).

The use of thresholds

Thresholds are being incorporated into methods used to manage, conserve, and understand ecosystems across the globe in different ways (Huggett 2005). Drinnan (2005) examined effects of fragmentation parameters on the persistence of frog, bird, fungi, and plant species, finding that remnant areas of habitat had clear threshold values for all taxa groups. Thresholds have also been used to show responses to disturbances on stream condition. In Michigan, Wang et al. (2008) used them to identify reference streams by comparing anthropogenic land use to drops in stream IBI scores and percent intolerant fish, using the point at which drops occurred to identify when the effects of land use begin to directly influence stream health. In the central plains, Evans-White et al. (2009) used them to measure the response of functional groups and assemblage in marcoinvertbrates to nutrient metrics in a stream, specifically carbon- phosphorus ratio, total phosphorus, and total nitrogen.

The use of thresholds has been criticized because of the potential for regional differences in response variables to the same predictor (Huggett 2005, Lindenmayer et al. 2005). To address this concern, I compared threshold breaks to results from other studies in the Midwest. In Wisconsin, as forest cover in the network catchment increased within watersheds, IBI scores increased as well (Wang et al. 1997). In reaches where forest cover was greater than 20%, few poor scores existed, while reaches with greater than 70% forest, no IBI scores under 40 existed (Wang et al. 1997), and these results were similar to the values that I used as breaks in scoring. Another study focused in eastern Wisconsin and western Michigan found that declines in IBI scores began to occur at 10-20% agriculture in the network riparian zone (Fitzpatrick et al. 2001), a value at which I observed the initial shift towards lower fish IBI scores. While Fitzpatrick et al. (2001) saw no score higher than fair after this initial decrease, this could be because some streams in their study region also had high levels of agriculture in their network catchments which was not a factor in the region. For some variables where thresholds were used to identify breaks, I did not have comparable studies within the region, but I believe the use of fish IBI scores and measured habitat variables specific to Michigan helped eliminate concern over regional bias.

Regional separation

The high scoring of many stream reaches at the network catchment landscape condition and the network riparian zone landscape condition filters indicate that streams of the region had habitat conditions suitable for the Arctic grayling. However, the northern Lower Peninsula, which contained nearly all the Arctic grayling's native range, had more than double the number of suitable reaches (13.40%) than the Upper Peninsula (6.19%), which had only one watershed where the species was described as existing historically. Given these results, I believe some regional separation based on geographical and possibly historical conditions occurred within the study region.

Management Implications and Future Needs

Conservation of the Arctic grayling

While this work suggests that habitat capable of supporting Arctic grayling exists within Michigan, biological factors, specifically competition with and predation from other species, may limit their successful reintroduction to the state. If a reintroduction were attempted in Michigan, it should be implemented following an adaptive approach. Goals should be based on ecological constraints as well as conservation objectives and social values, and reintroductions should be planned carefully following techniques shown to be successful in other areas (i.e., identification of potential spawning areas and use of remote site incubators). Further, research projects focused on the greatest research needs specific to understanding the Arctic grayling, such as the effects of predation and competition by brown and rainbow trout as well as habitat use in different life stages, should be conducted concurrently with reintroductions. Following an adaptive management approach would ensure that if a reintroduction attempt failed, we can still learn about the life history and biological interactions of the Arctic grayling, improving future chances for reintroductions and range expansion in Michigan and other areas.

With the potential for a changing climate to alter ecosystem structure and function across the globe (IPCC 2007) coupled with increasing human population and demands for natural resources (Helfman 2007), subpopulations like the Montana Arctic grayling occurring at southern ends of their range are at potentially greater risk for extirpation. The upper Missouri River is largely fed by snowmelt, controlling both temperature and flow conditions (Lamothe and Peterson 2007). Western mountain ranges are predicted to have decreased snowpack in the future (IPCC 2007), which may result in flashier stream conditions during winter months. In the summer, snowmelt may no longer be available to stabilize flows and lower temperatures through the entire season. The upper Missouri

River, thought to have been a glacial refugia for the grayling because of its stable flows and cold temperatures, may no longer possess the characteristics needed to support the Arctic grayling.

The effects of climate change on Michigan streams will vary depending on main sources of water to the stream. Streams dominated by groundwater input will potentially have lesser increases in temperature with increasing air temperatures, because groundwater is stored below the surface and cools before entering the stream (Stefan and Preud'homme 1993). Unlike snowpack-driven streams which may become less stable due to changes in timing and amount of input from snowmelt, groundwater driven systems will continue to maintain stable flows, given precipitation changes are not dramatic. The Michigan streams we identified as high rating are controlled by groundwater input and therefore may maintain their cooler temperatures and stable flows (Stefan and Preud'homme 1993, Steen et al. 2010). Based on the premise that suitable habitat remains in Michigan, and if effects of climate change are determined to be less severe in groundwater- vs. snowmelt-driven systems, reintroductions of Arctic grayling to Michigan could be critical for supporting the conservation of this species in its native range within the United States.

The assessment method

Overall, the method developed to answer the question of whether fluvial habitat capable of supporting the Arctic grayling exists in Michigan was effective and holds promise as an approach that may be applicable to for reintroduction, conservation, and management of many species with specific habitat requirements. Establishing habitat needs specific to grayling such as stable flows, high baseflows, and low gradients, helped identify locations that are most suitable, as well as offering insights into why previous reintroduction attempts in reaches with less suitable habitat conditions may have failed. Further, determining how landscape factors, specifically drainage area, geology, and wetlands in the network riparian zone predict habitat conditions, helped improve overall understanding of landscape effects in my study region while also improving the assessment tool. By accounting for habitat suitability of a reach in the context of overall connectivity with other suitable reaches, I created a final rating that helped classify habitat for a species that typically moves long distances within the year, a factor that is often not considered in fisheries management (Fausch 2002).

The assessment tool itself is adaptable; new research can lead to the alteration and improvement of habitat identification. This would allow for information acquired through adaptive management approaches to be incorporated to better predict grayling habitat. For instance, if brown trout predation is found to be a limiting factor on graying survival, a biotic filter showing the presence of brown trout could be included at the reach scale, eliminating those reaches that contain the species. While easily adaptable, my approach remains both time and cost efficient if landscape datasets are available and landscape to habitat relationships are understood.

The assessment method that I developed to rank stream segments based on habitat quality specific to the Arctic grayling may be a beneficial tool in the location of habitat for other species that may be range-restricted or locally extinct. For instance, the reintroduction of brook trout range in Illinois is currently being considered by Illinois Department of Resources (Hinz et al. unpublished). Brook trout were once believed to exist within several northern stream systems in Illinois, but have been eliminated except for Lake Michigan (Hinz et al. unpublished). Using the available information specific to brook trout life history, the best possible streams for reintroduction could be indentified using our multiple scale filter approach (Hinz et al. unpublished).

As GIS landscape data and modeled reach variables become more available, development and application of management tools like ours represents a step towards more time and cost efficient approaches. The assessment tool is easily interpretable and can be related to stakeholders and the public, supplying clear justification for where and why reintroductions were made. I believe my method of assessing grayling habitat suitability is useful for identifying if and where a range restricted or locally extinct species could possibly be sustained within a region.

Table 3.1: Scores applied to each stream reach over all five filters. Two indicates suitable, 1 is marginal, while 0 is considered unsuitable for Arctic grayling.

Scale	Variable	Suitability rank		
		2	1	0
Network watershed				
	Drainage area (km^2)	40.00 - 620.00	<40.00 or > 620.00	----
	Coarse geology (%)	>80.00	50.00-80.00	<50.00
	Forest land cover (%)	>60.00	30.00 -60.00	<30.00
Network riparian zone				
	Wetlands land cover (%)	>25.00	<25.00	-----
	Urban land use (%)	<5.00	5.00-15.00	>15.00
	Agriculture land use (%)	<10.00	10.00 -40.00	>40.00
Reach				
	Gradient	0.0009-0.0030	0.0031-0.0100	> 0.0100 or <0.0009
	10/90 ratio	<10.00	10.00-20.00	>20.00
	90/50 ratio	>0.55	0.25-0.55	<0.25
	July mean temperature (C°)	<16.00	16.00-20.00	>20.00

Table 3.2: Variables included in the stream segment rating tool. The reason for including each variable is described briefly, and the sources of data and literature used to create suitability scorings are listed.

Scale	Variable	Purpose	Data/literature source
Network watershed			
	Drainage area (km^2)	Greater depth for cover, less competition with brook trout	Krueger (1981), Vincent (1962)
	Coarse geology (%)	Greater potential for stable flows and cold stable temperatures	Seelbach et al (2007)
	Forest land cover (%)	Greater potential for high quality habitat	Relationship between fish IBI and forest, Wang et al.(1997)
Network riparian zone			
	Wetlands land cover (%)	Greater stream flow stability with more wetlands in the network riparian zone, as well as a decrease in fine sediments within the stream channel	Relationships between visual stream stability metric and wetlands, Tingley (this manuscript), Cohen and Brown (2007)
	Urban land use (%)	Greater potential for degraded habitat	Relationship between fish IBI and urban
	Agricultural land use (%)	Greater potential for degraded habitat	Relationship between IBI and agriculture, Fitzpatrick et al. (2001)
Reach			
	Stream gradient	Arctic grayling prefer low to moderate gradients	Vincent (1962), Liknes and Gould (1981)
	10/90 ratio	Arctic grayling prefer streams with stable flow all season	Infante (2006), Seelbach et al. (2007), Vincent (1962)
	90/50 ratio	Indicates greater depth for cover	Raleigh (1982), Raleigh (1986), Vincent (1962)
	July mean temperature(C°)	Arctic grayling Maximum critical temperatures ranging from 20.0 (Alaska) to 25.0° C (Montana); USFWS habitat suitability index shows optimal growth between 7.5 and 16° C	Hubert et al. (1985), Lohr et al. (1996), Lamothe and Peterson (2007)

Table 3.3: Length of connected stream segments and the re-ranked score given based on individual reach habitat score

Individual reach habitat score	Total length of connected reaches (km)	Individual reach connectivity score
> 8		
	0 to 10	0
	10 to 100	1
	>100	2
5 - 8		
	< 100	0
	> 100	1
< 5		
	All	0

Table 3.4: Mean, range and standard deviation (SD) of variables used as filters in the assessment tool throughout the study region.

Scale	Variable name	Mean	Range	SD
Network catchment				
	Drainage Area (km^2)	170.84	0.02-10373.28	718.18
	Forest land cover (%)	59.96	0.00-100.00	22.91
	Coarse geology (%)	71.30	0.00-100.00	37.98
Network riparian zone				
	Urban land use (%)	1.71	0.00-60.47	3.08
	Agricultural land use (%)	5.76	0.00-95.29	12.66
	Wetlands land cover (%)	37.18	0.00-1.00	25.54
Reach				
	Stream gradient (%)	0.78	0.00-18.06	1.09
	10/90 flow ratio	16.30	1.13-640.92	25.82
	90/50 flow ratio	0.37	0.04-0.97	0.15
	July mean temperature (C°)	16.38	4.70-24.50	0.15

Table 3.5: Final rating of a selection of stream segments including top ranked segments, segments where reintroductions were performed, and a collection of other segments where stream field data were available. River segments marked with * are those that historically contained Arctic grayling and a voucher specimen. Those marked with ** are streams where a historical record or written account of Arctic grayling occurs but a voucher specimen does not exist.

River segment		Peninsula	Watershed	Final rating
Top rated				
	Little Manistee River**	Lower	Manistee	1.70
High rated				
	Pine River*	Lower	Manistee	1.42
	Sturgeon River *	Lower	Cheboygan	1.41
	Upper White River**	Lower	Pere Marquette-White	1.39
	Sucker River	Upper	Betsey-Chocolay	1.38
	Pere Marquette River**	Lower	Pere Marquette-White	1.32
	Upper Au Sable River*	Lower	Au Sable	1.30
Former reintroduction sites				
	Upper Manistee River**	Lower	Manistee	1.21
	Huron River	Upper	Dead-Kelsey	0.97
	Mulligan Creek	Upper	Dead-Kelsey	0.96
	Middle Au Sable River**	Lower	Au Sable	0.76
	Cedar River	Lower	Boardman	0.54
	Section 34	Upper	Betsey-Chocolay	0.00
	Spray Creek	Upper	Betsey-Chocolay	0.00
Other sites with field data				
	Black River**	Lower	Black	1.28
	Jordan River*	Lower	Boardman-Charlevoix	1.15
	Otter River*	Upper	Sturgeon	1.04
	Two Hearted River	Upper	Betsey-Chocolay	0.97
	Upper Muskegon River	Lower	Muskgeon	0.89
	Sturgeon River*	Upper	Sturgeon	0.78
	Rifle River	Lower	Au Gres-Rifle	0.74
	Pigeon River	Lower	Cheboygan	0.50
	Ocqueoc River	Lower	Lone-lake Ocqueoc	0.00

Table 3.6: Percent of geomorphic units averaged across sites in top-ranked stream segments.

River segment	Pool	Riffle	Run
Little Manistee River	7.36	8.58	84.06
Pine River	5.89	21.48	72.63
Sturgeon River	1.33	40.67	58.00
Sucker River	4.83	4.82	90.35
Pere Marquette River	6.01	2.19	91.80
Upper Au Sable River	2.16	4.14	93.69

Table 3.7: Riffle substrate composition and embeddedness averaged over all riffles within each high rated stream segment.

River segment	Riffle substrate composition (%)						Embeddedness (%)	
	Sand	Fine gravel	Coarse gravel	Cobble	Boulder	Clay	Fine gravel	Coarse gravel
Little Manistee River	40.63	6.25	45.31	7.81	0.00	0.00	31.25	24.60
Pine River	31.15	2.50	17.12	42.38	5.71	1.14	50.00	32.12
Sturgeon River	1.02	1.04	56.82	41.11	0.00	0.00	75.00	35.23
Sucker River	39.29	27.68	12.50	14.29	0.00	16.25	70.83	50.00
Pere Marquette River	20.00	30.00	30.00	10.00	0.00	10.00	50.00	50.00
Upper Au Sable River	25.00	12.50	62.50	0.00	0.00	0.00	30.00	15.83

Table 3.8: Mean and maximum depth, average bank stability, average in stream cover and overhanging vegetation for all pools in high rated stream segments.

River segment	Depth (m) Mean	Max	Bank stability	Overhanging vegetation (%)	Cover (%)
Little Manistee River	0.74	2.50	3.33	33.33	17.27
Pine River	0.57	1.40	3.17	62.50	20.00
Sturgeon River	0.51	1.00	2.67	50.00	10.67
Sucker River	0.80	1.30	3.19	58.33	32.96
Pere Marquette River	0.64	1.70	3.10	37.80	19.69
Upper Au Sable River	0.66	1.30	3.33	41.67	20.33

Table 3.9: Mean and maximum depth, average bank stability, and average in-stream cover for all runs in high rated stream segments. The average percent of left and right transect points (stream margins) in which silt was the dominate substrate type is also presented.

River segment	Depth (m) Mean	Depth (m) Max	Bank stability	Cover (%)
Little Manistee River	0.60	1.40	3.52	17.96
Pine River	0.60	2.10	3.12	12.73
Sturgeon River	0.40	1.20	3.39	17.31
Sucker River	0.44	1.80	2.98	28.59
Pere Marquette River	0.74	2.00	3.35	17.62
Upper Au Sable River	0.67	1.70	3.62	18.58

Table 3.10: Presence of fish species that could act as competitors or predators of the Arctic grayling within high rated stream segments. Those species marked with as "X" were present in sampling efforts. Fish assemblage data were obtained from the Michigan Department of Natural Resources (DNR) Fish Collection System and Michigan River Inventory databases (Seelbach and Wiley, 1997).

Species		**Stream Segment**					
		Little Manistee	Upper Au Sable	White River	Sucker River	Pere Marquette River	Pine River
Brook trout	*Salvelinus fontinalus*	X	X	X	X	X	X
Brown trout	*Salmo trutta*	X	X	X	X	X	X
Rainbow trout	*Oncorhynchus mykiss*	X	X		X	X	X
Salmon spp.	*Salmo spp.*	X			X	X	
Northern pike	*Esox lucius*					X	X
Largemouth bass	*Micropterus salmoides*					X	

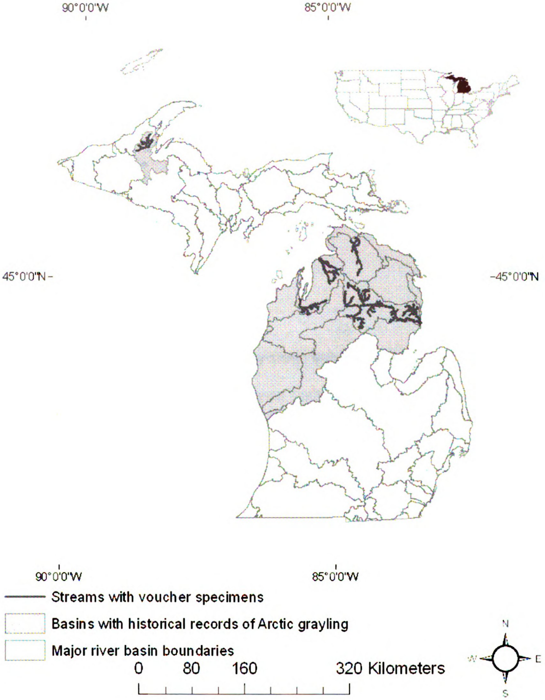

Figure 3.1: Major river basins of Michigan historically inhabited by the Arctic grayling (Vincent 1962) with streams from which voucher specimens were collected indicated (Bailey et al. 2004).

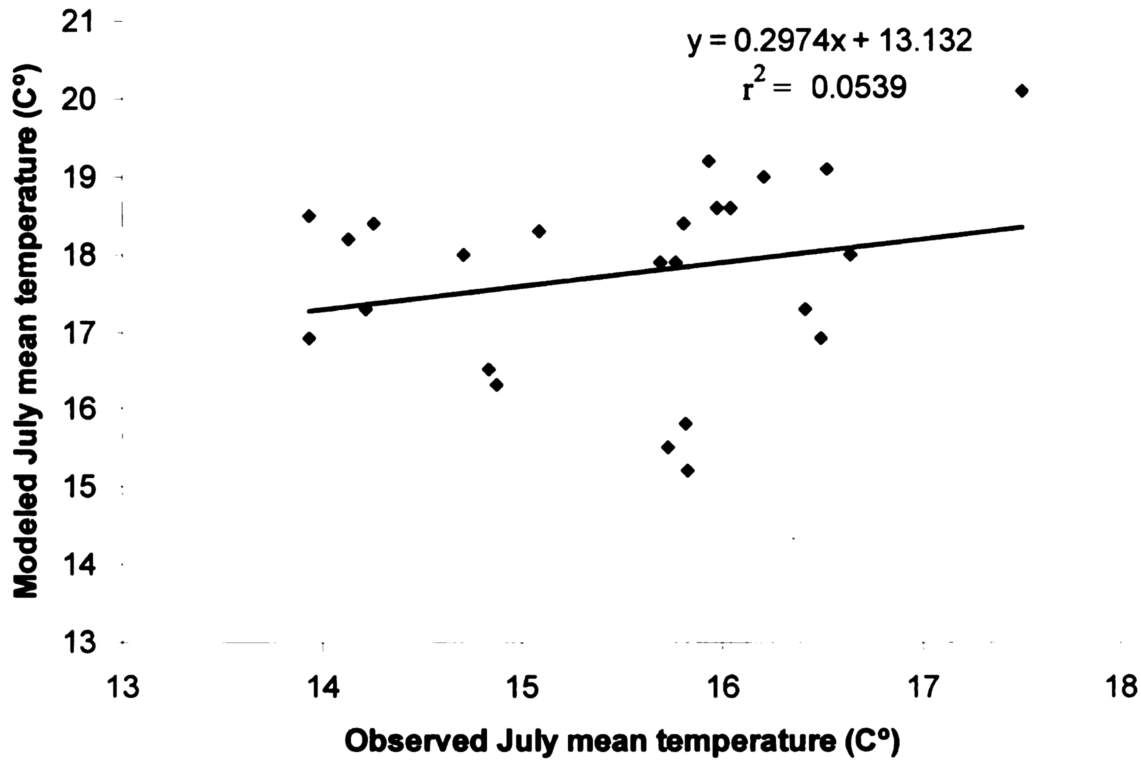

Figure 3.2: Comparison of modeled July mean temperatures with measured July means for 26 sites in northern Michigan. Modeled temperatures tended to be overestimated for 2009.

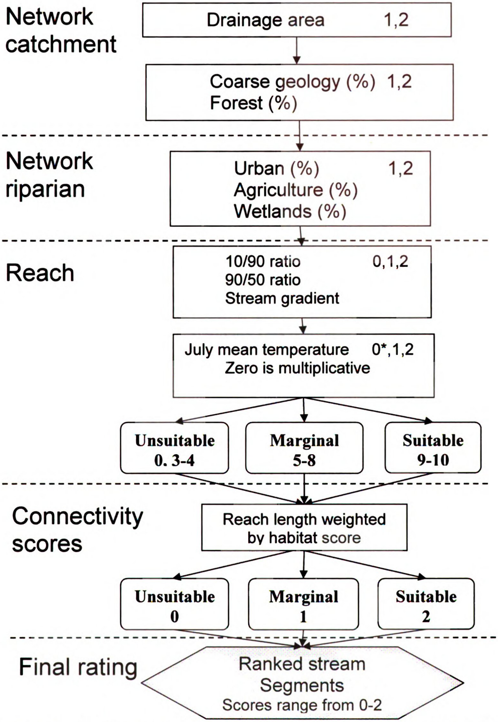

Figure 3.3: Habitat assessment tool used to rate stream segments within Michigan as the most likely to support a population of Arctic grayling. I organized the assessment over 3 scales, the network catchment, network riparian zone, and reach inclusive of 5 filters including drainage area, catchment landscape condition, riparian zone landscape condition, reach condition, and temperature. After the cumulative scoring of a reach, I rescored based on total connectivity and habitat score then rated a stream segment on total length of unsuitable, marginal, and suitable reaches.

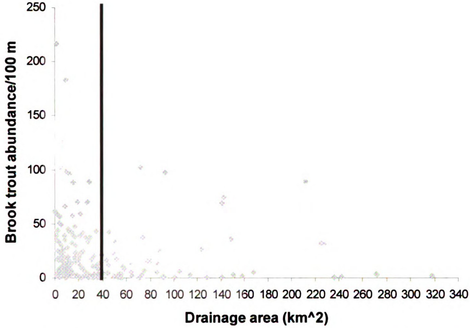

Figure 3.4: Brook trout abundance in stream reaches of my study region plotted against drainage area. As drainage area increases, brook trout abundance decreases, with a marked decrease in numbers occurring at 40 km^2.

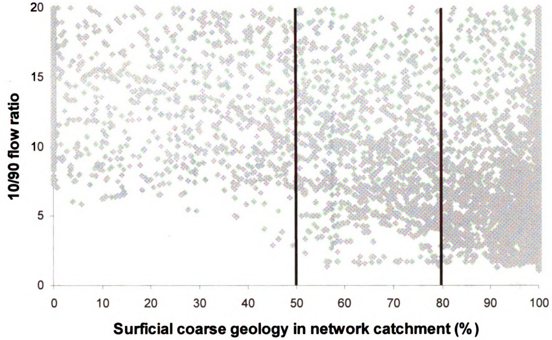

Figure 3.5: 10/90 ratio versus network catchment coarse geology (%) for all reaches in Michigan. Reaches with coarse geology percentages less than 50% generally have 10/90 ratios greater than 8; reaches with coarse geology between 50 and 80% show a decrease in minimum 10/90 ratio values, and those values greater than 80% have a minimum value of about 2.

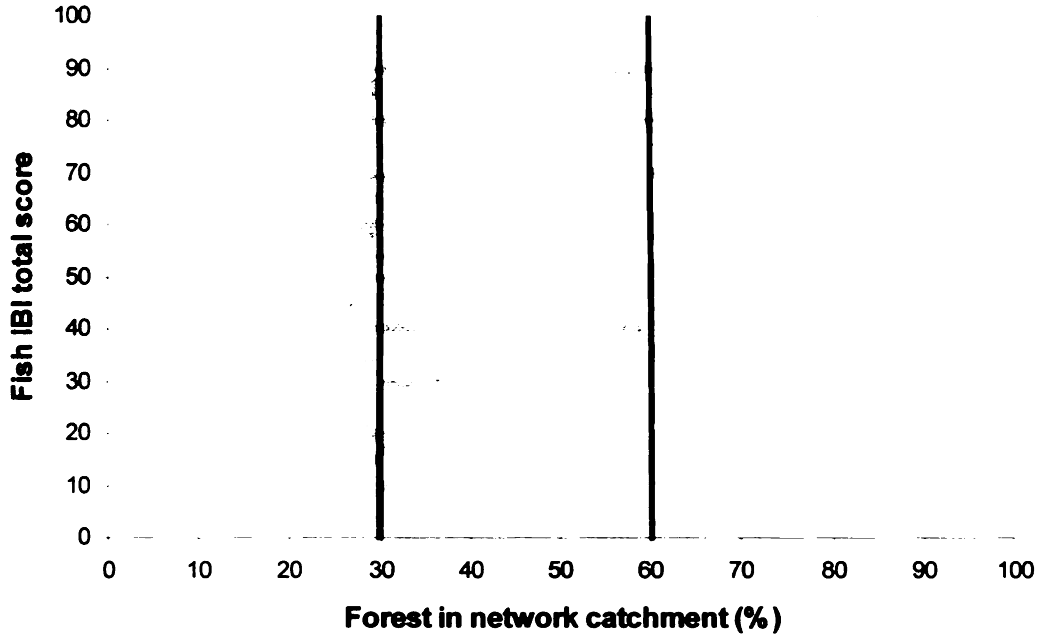

Figure 3.6: Fish Index of Biotic Integrity (IBI) total score versus forest in the network catchment (%) across Michigan. Less than 30% forest is related to increased numbers of sites with low scores. At 30 to 60%, the number of low scores decreases, and few sites with greater than 60% forest have an IBI less than 40.

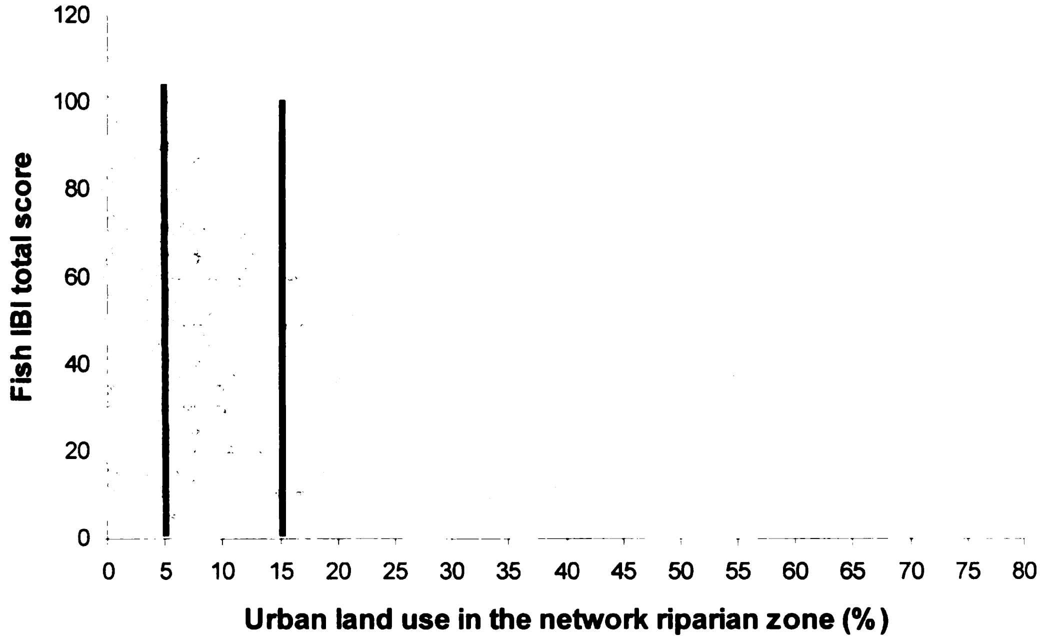

Figure 3.7 Fish Index of Biotic Integrity (IBI) total score versus urban land use in the network riparian zone (%) across Michigan. At 6%, sites show marked decrease in IBI score, with few values above 70 present. At 15%, only one value exists above 60.

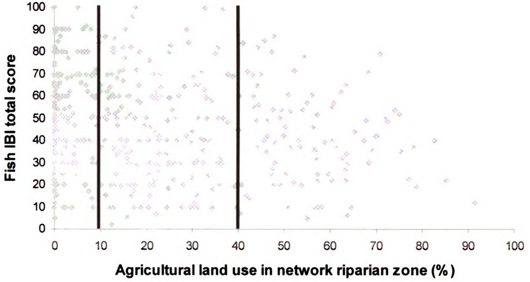

Figure 3.8: Fish Index of Biotic Integrity (IBI) total score versus agriculture in the network riparian (%) across Michigan. Sites with agricultural values of 10 to 40% show a decline in IBI score overall, and at 40%, values of agriculture drop sharply.

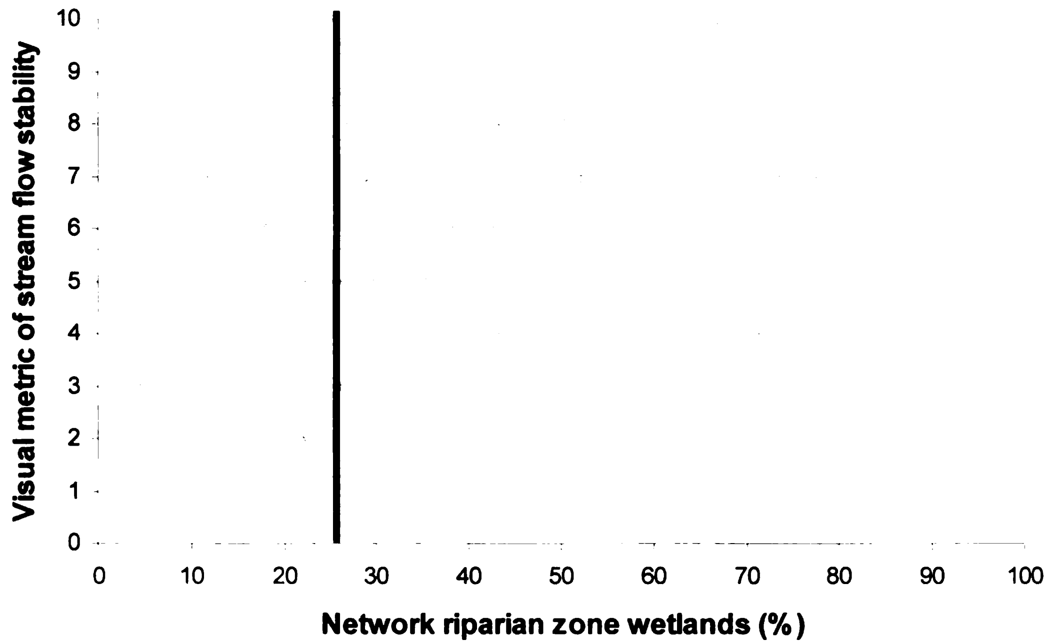

Figure 3.9: Visual metric of stream flow stability versus network riparian zone wetlands (%). Sites scored 8 or higher first appear with more than 25% wetlands, and sites with less than 4 do not occur at about 25% wetlands.

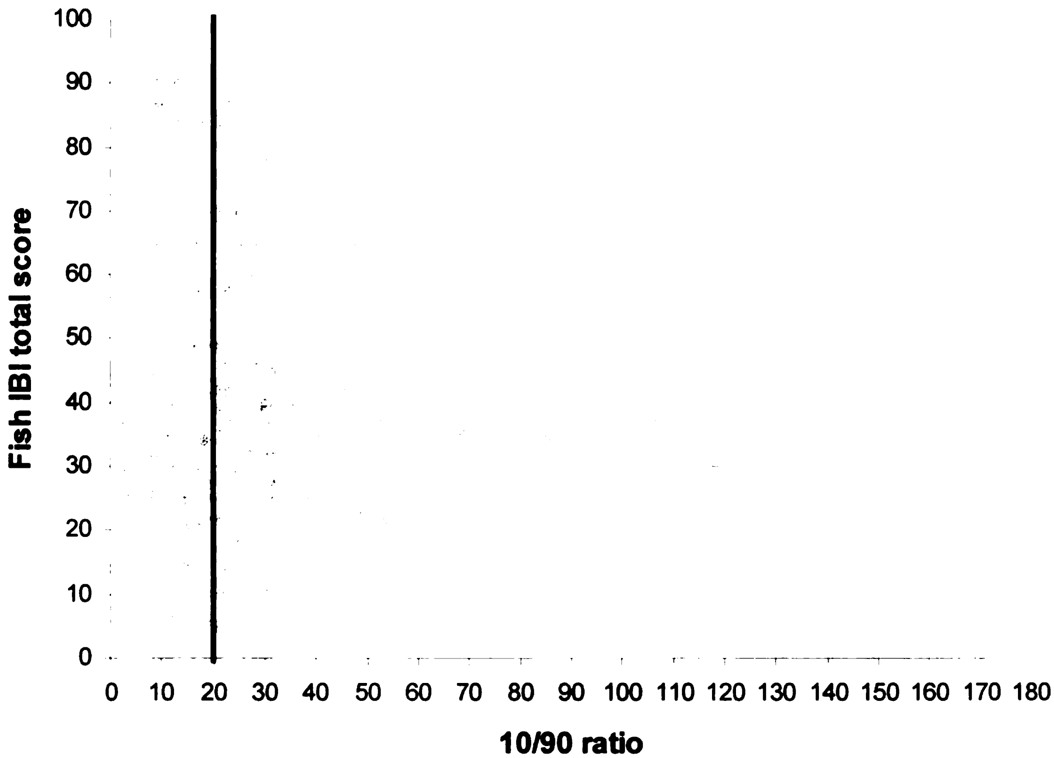

Figure 3.10: Fish Index of Biotic Integrity (IBI) total score plotted against 10/90 flow ratio in Michigan. IBI scores decrease at a 10/90 ratio of 20.

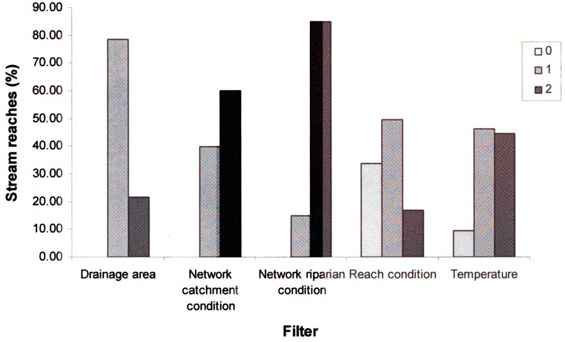

Figure 3.11: Percent of stream reaches scoring a 0, 1, or 2 at each hierarchical filter. Note that only reach condition and temperature could score a 0. Landscape variables seem to be overall suitable across segments, while drainage area and reach condition (10/90 ratio, 90/50 ratio, and gradient) seem to be the most limiting filters.

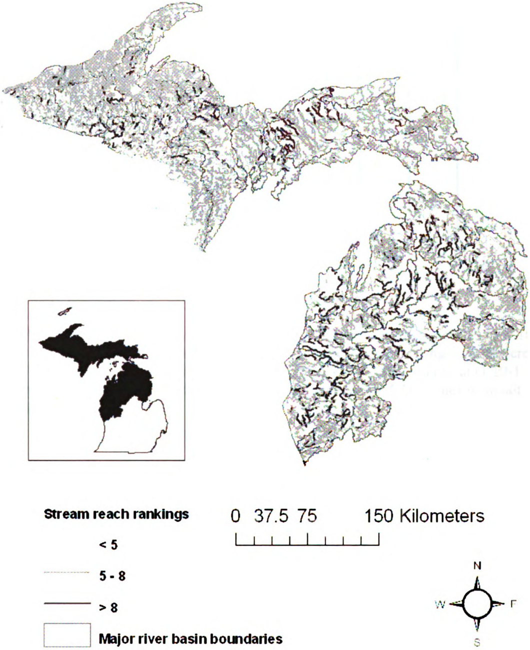

Figure 3.12: Rating of individual stream reaches before application of connectivity. The majority of high ranked reaches occur in the Lower Peninsula, while in the Upper Peninsula the number of high scoring reaches is lower.

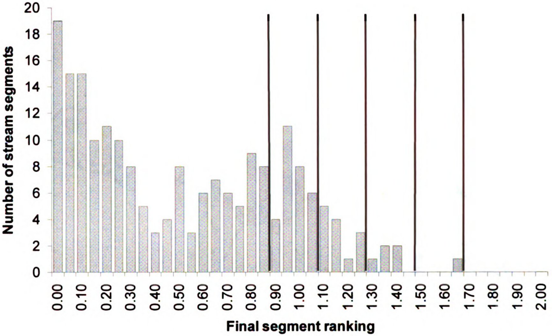

Figure 3.13: Frequency distribution of final stream segment rankings grouped by 0.10 changes in segment score. Black lines indicate breaks between groupings. Sites were grouped by final rating score into top (1.50-1.70), high (1.30-1.49), marginal (1.10-1.29), low (0.90-1.09), and lowest (0.00-0.89). Stream segments with 0.00 values were not included within this figure.

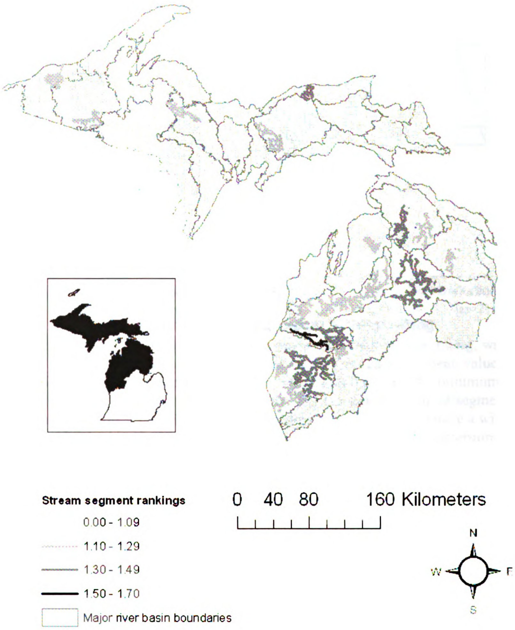

Figure 3.14: Final rating of stream segments across Michigan. The majority of high rankings streams occurs in the Lower Peninsula.

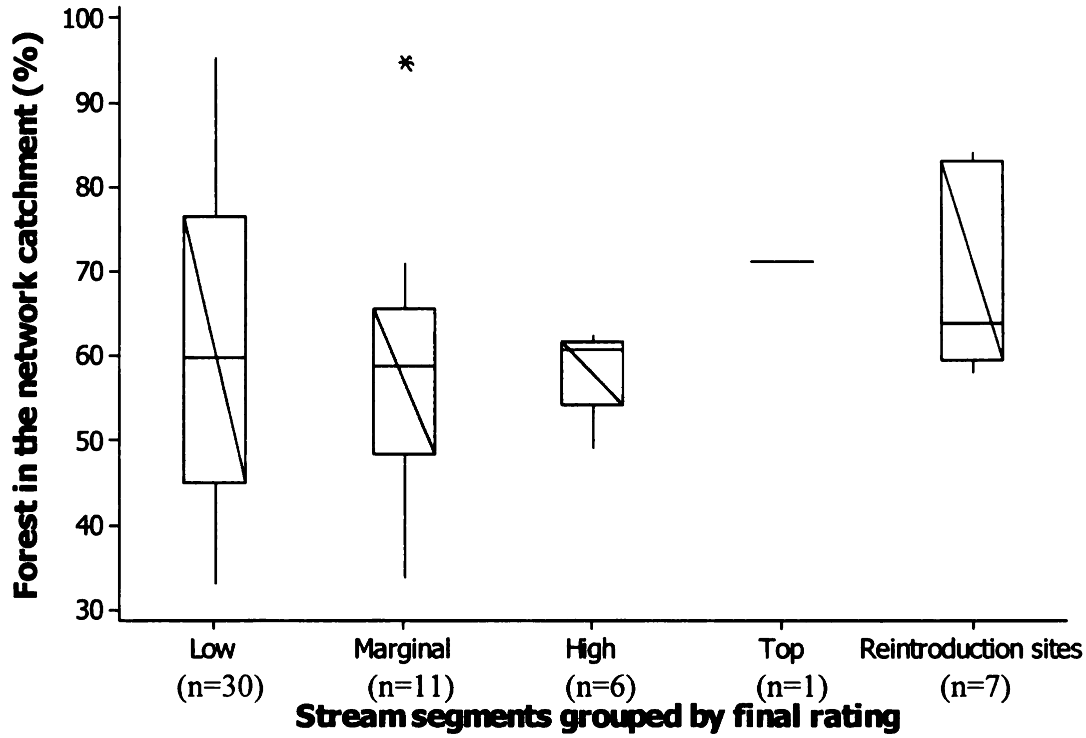

Figure 3.15: Descriptive statistics for stream segments grouped by final rating, with statistics for reintroduction sites also shown. Horizontal bars represent mean values, boxes represent the lower and upper quartiles, vertical bars represent the minimum and maximum scores, and asterisks represent outliers. The top ranked group of segments has the highest mean of forest land cover. Reintroduction sites are shown to have a wide range in forest land cover, but the mean falls above 60%, the percentage determined to be suitable for Arctic grayling.

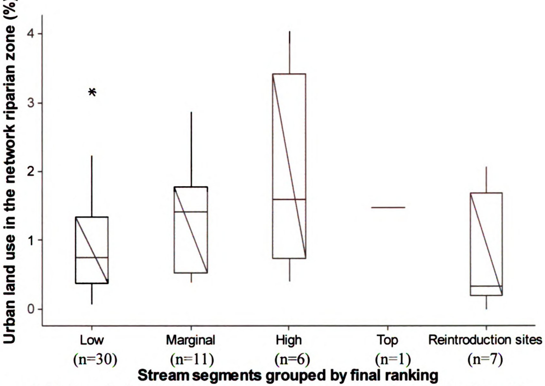

Figure 3.16: Descriptive statistics for stream segments grouped by final rating, with statistics for reintroduction sites also shown. Horizontal bars represent mean values, boxes represent the lower and upper quartiles, vertical bars represent the minimum and maximum scores, and asterisks represent outliers. All values fall in the suitable range of urban land use (less than 5%) within my study region.

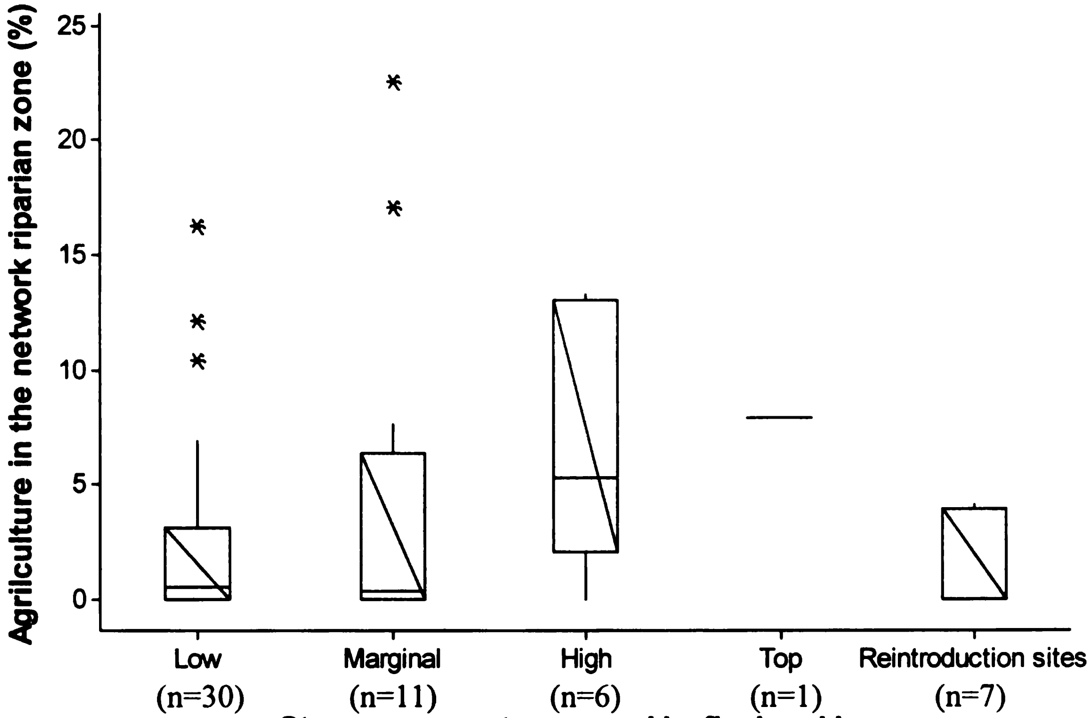

Figure 3.17: Descriptive statistics for stream segments grouped by final rating, with statistics for reintroduction sites also shown. Horizontal bars represent mean values, boxes represent the lower and upper quartiles, vertical bars represent the minimum and maximum scores, and asterisks represent outliers. Reintroduction sites have the lowest mean agricultural percentage, while the top ranked site have the highest average, yet is below 10%, the break point between good and suitable ranges.

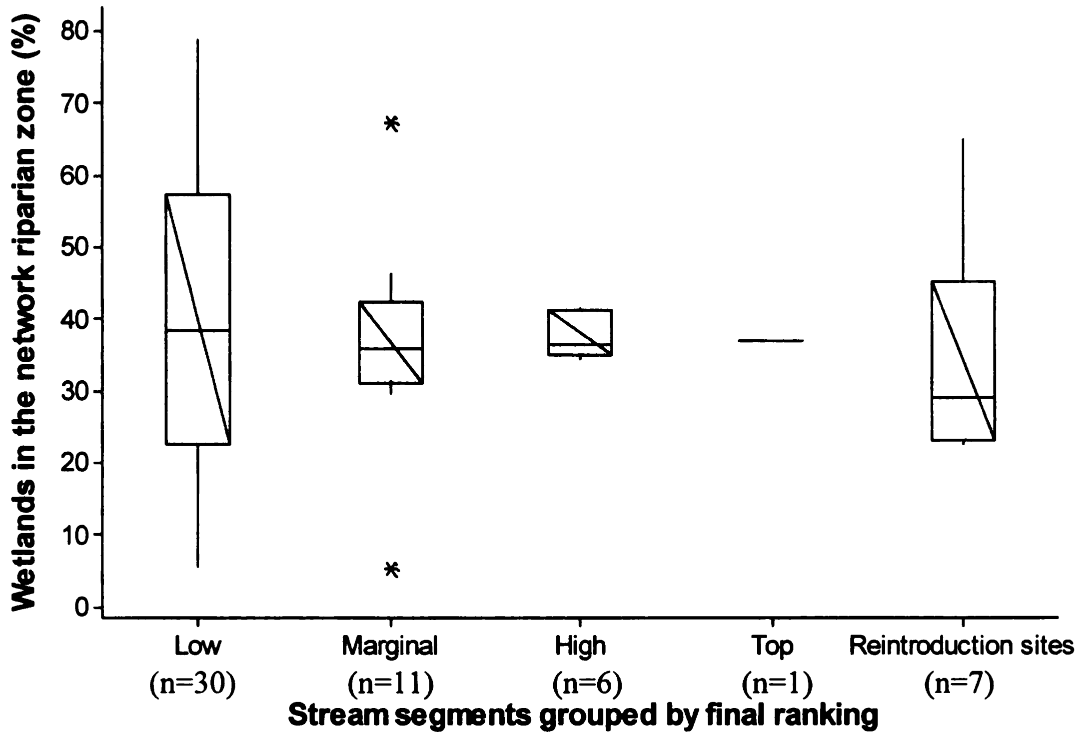

Figure 3.18: Descriptive statistics for stream segments grouped by final rating, with statistics for reintroduction sites also shown. Horizontal bars represent mean values, boxes represent the lower and upper quartiles, vertical bars represent the minimum and maximum scores, and asterisks represent outliers. All mean values are above 25%, but low segments have some variation below 25%, while marginal segments has one segment that has less than 25% wetlands present.

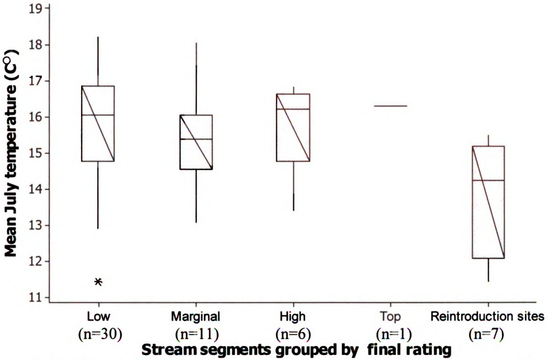

Figure 3.19: Descriptive statistics for stream segments grouped by final rating, with statistics for reintroduction sites also shown. Horizontal bars represent mean values, boxes represent the lower and upper quartiles, vertical bars represent the minimum and maximum scores, and asterisks represent outliers. All mean temperatures fell close to the suitable range of less than 16°C, while lower ranked segments and reintroduction sites have high variance.

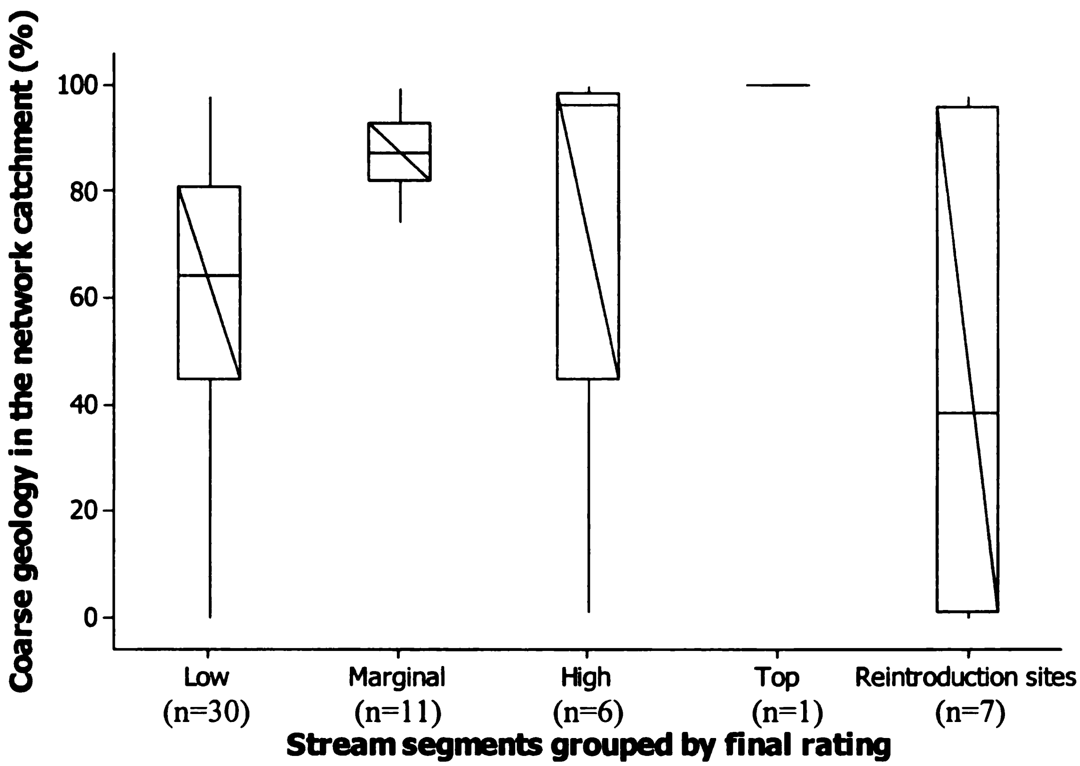

Figure 3.20: Descriptive statistics for stream segments grouped by final rating, with statistics for reintroduction sites also shown. Horizontal bars represent mean values, boxes represent the lower and upper quartiles, vertical bars represent the minimum and maximum scores, and asterisks represent outliers. With increasing coarse geology, average group scores increase. Reintroduction segments have highly variable scores ranging from poor to suitable. Stream segments in the low rated group had high variation in coarse geology as well.

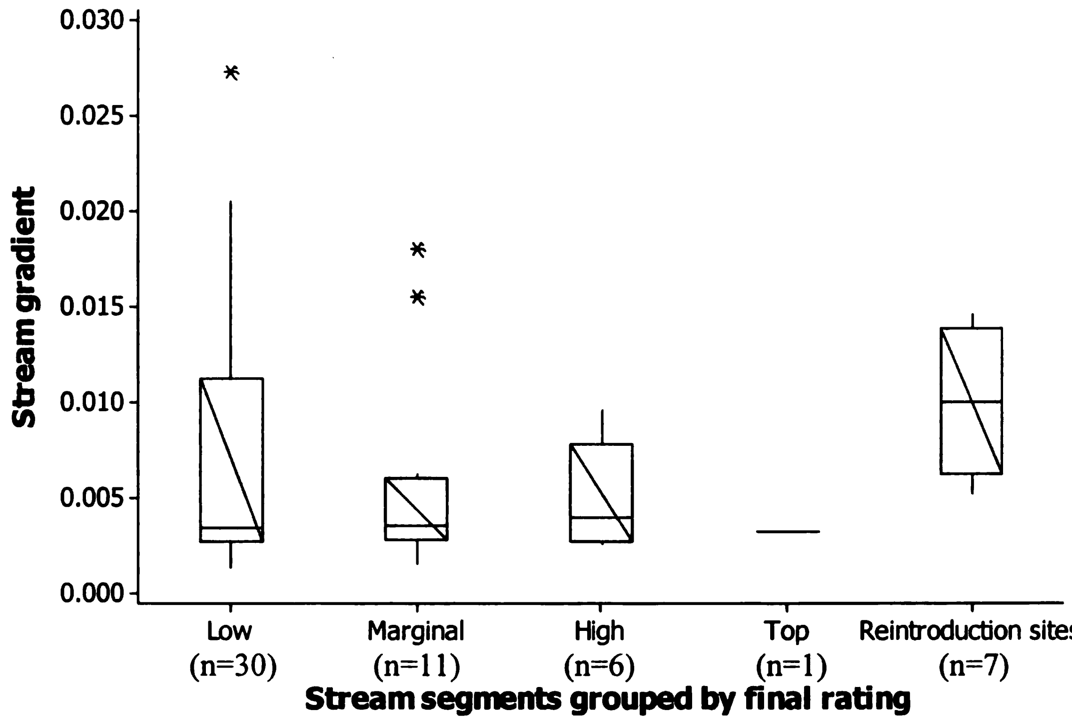

Figure 3.21: Descriptive statistics for stream segments grouped by final rating, with statistics for reintroduction sites also shown. Horizontal bars represent mean values, boxes represent the lower and upper quartiles, vertical bars represent the minimum and maximum scores, and asterisks represent outliers. Mean values were similar among ranked stream segments, but as rankings decreased groups varied more. Reintroduction sites had a higher mean gradient than what is considered the upper limit for marginal (0.010) with rankings as high as 0.0170.

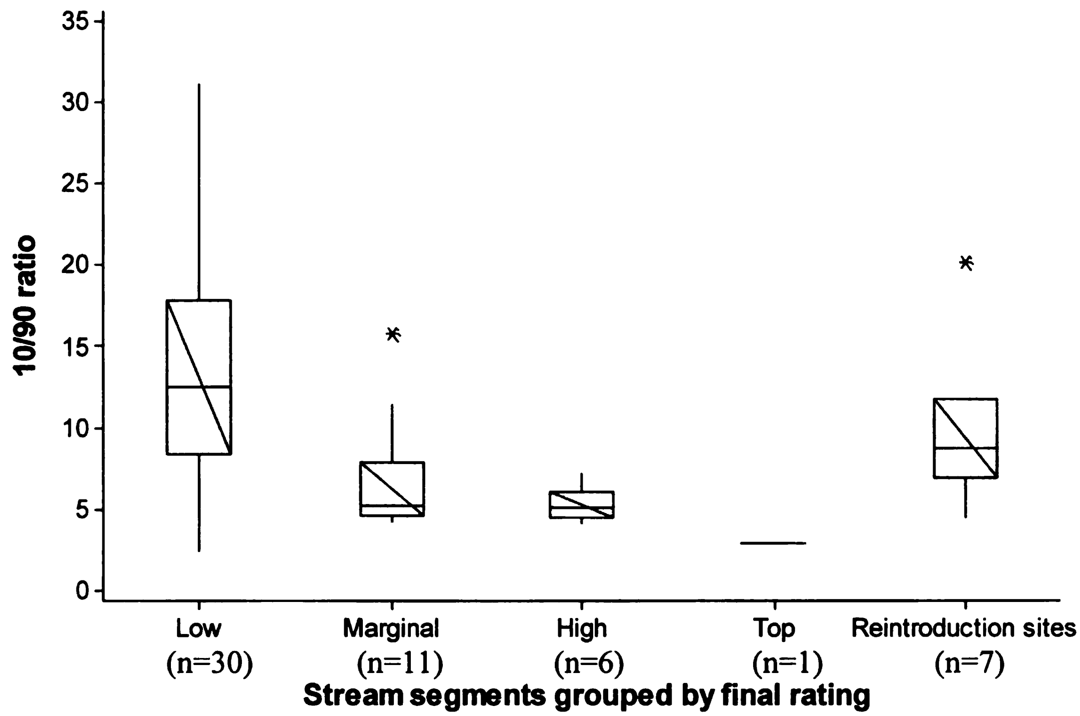

Figure 3.22: Descriptive statistics for stream segments grouped by final rating, with statistics for reintroduction sites also shown. Horizontal bars represent mean values, boxes represent the lower and upper quartiles, vertical bars represent the minimum and maximum scores, and asterisks represent outliers. A general trend of decreasing mean values and variance in 10/90 ratio occurs as stream segments increase in rank. Reintroduction sites had a mean 10/90 ratio that was suitable (<10), but had segments that were poor and marginal as well.

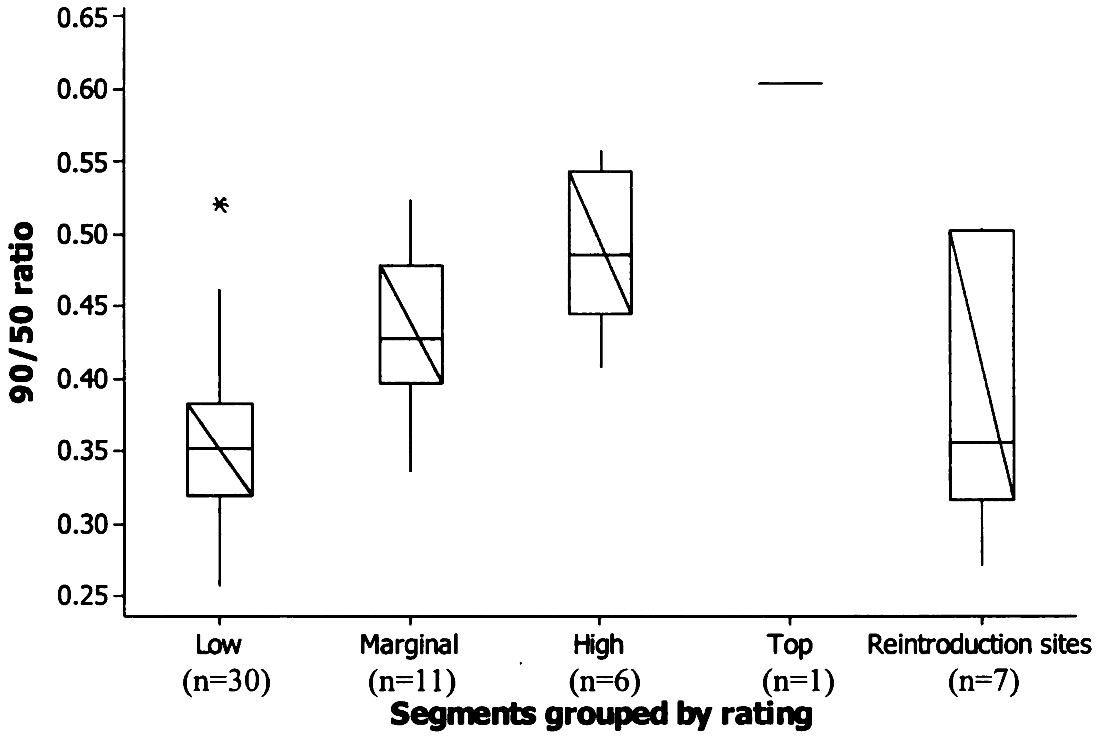

Figure 3.23: Descriptive statistics for stream segments grouped by final rating, with statistics for reintroduction sites also shown. Horizontal bars represent mean values, boxes represent the lower and upper quartiles, vertical bars represent the minimum and maximum scores, while asterisks represent outliers. A general trend of increasing mean values and variance of 90/50 ratio occurs as stream segments increase in rank. Reintroduction sites had a mean 90/50 ratio well below the good score of 55%.

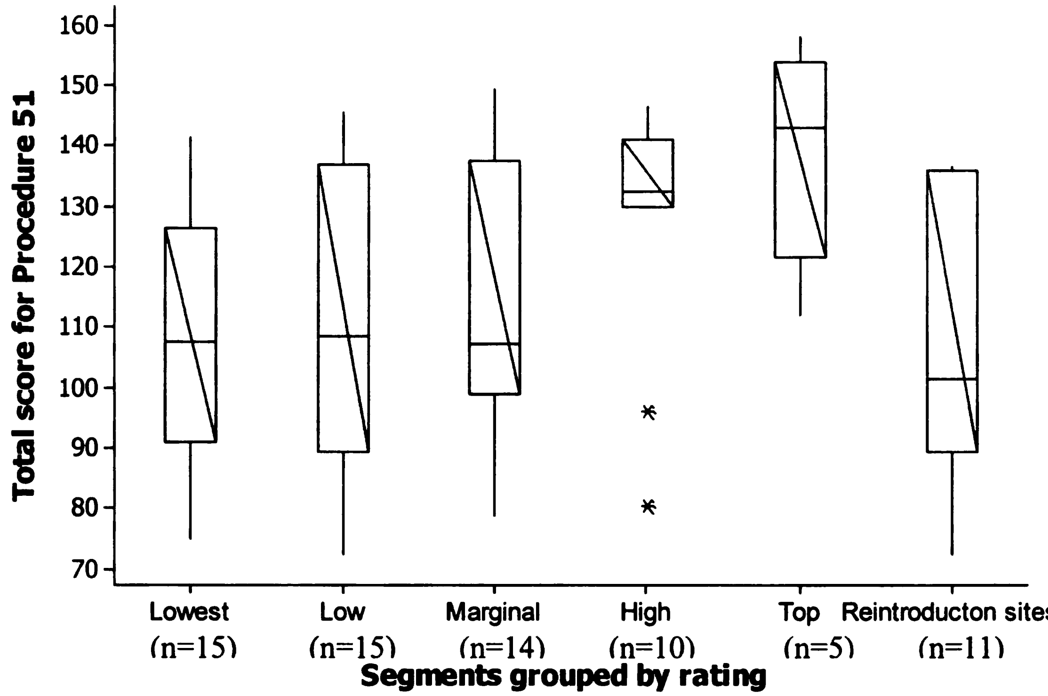

Figure 3.24: Descriptive statistics for stream segments grouped by final rating, with statistics for reintroduction sites also shown. Horizontal bars represent mean values, boxes represent the lower and upper quartiles, vertical bars represent the minimum and maximum scores, while asterisks represent outliers. Top and high rated segments have higher mean Procedure 51 total score values than those with below high and reintroduction sites, which all have means close to 100. Cutoff for "good" total Procedure 51 total scores is 105.

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APPENDIX

APPENDIX A: Correlations among landscape variables

Table A.1: Correlations among landscape variables

	DA	LR Wet	NW Wet	NR Wet	LW Wet	Grad	Coarse	LW Ag	LR Ag	NR Ag	NW Ag	LW For	NW For	LR For
DA														
LRWet	0.18													
NWWet	0.04	0.30												
NRWet	0.05	0.46	0.59											
LWWet	0.02	0.59	0.67	0.43										
Grad	**-0.59**	-0.49	-0.18	-0.22	-0.34									
Coarse	0.11	-0.06	-0.48	-0.17	-0.39	-0.02								
LWAg	0.01	-0.02	0.04	-0.15	0.08	-0.14	-0.06							
LRAg	-0.11	-0.23	-0.02	-0.23	-0.09	-0.01	-0.05	0.80						
NRAg	-0.03	-0.24	-0.15	-0.35	-0.13	0.06	-0.15	0.48	0.44					
NWAg	0.27	0.05	-0.12	-0.07	-0.05	-0.26	-0.07	0.58	0.44	0.75				
LWFor	0.00	-0.45	-0.48	-0.32	**-0.74**	0.35	0.33	-0.53	-0.28	-0.08	-0.25			
NWFor	-0.03	-0.19	**-0.69**	-0.46	-0.49	0.20	0.45	-0.30	-0.19	-0.23	-0.35	0.67		
LRFor	-0.17	**-0.93**	-0.27	-0.36	-0.53	0.53	0.11	-0.19	-0.02	0.15	-0.16	0.52	0.20	
NRFor	-0.22	-0.47	-0.52	**-0.64**	-0.36	0.44	0.08	-0.05	0.08	0.14	-0.21	0.42	0.62	0.44