Regional Stream Classification Frameworks and Biotic Homogenization in Streams of the Midwest: An Evaluation Using Landscape-Scale Patterns in Fish Communities

Report No. 139 of the
Kansas Biological Survey

2006

By

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Submitted to the Department of Ecology and Evolutionary Biology and the Faculty of the Graduate School for the University of Kansas in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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Date Defended: **06-29-06**

The Dissertation Committee for Bridgett R.K. Chapin certifies that this is the approved version of the following dissertation:

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ABSTRACT

This dissertation includes three studies that explored landscape-scale patterns in reference stream fish communities in Kansas, Missouri, Nebraska and Iowa (U.S.A.) to inform the design of classification frameworks for streams, and to elucidate important mechanisms that shape stream ecosystems in this region.

The development of regional stream classification frameworks is a work in progress. Much debate addresses whether more terrestrially or more aquatically–defined frameworks better explain landscape-level ecological variation in streams. Chapter One addressed this and other issues by comparing the classification strengths (CS) of 8 *a priori* and *a posteriori* classification frameworks for streams at two scales. CS was based on the difference between mean within-group fish community similarity and mean among-group similarity (Sorenson and Bray-Curtis similarity indices) within each framework. The *a priori* frameworks included: Strahler order; Hydrologic Unit Codes (HUCs) or “watersheds”; two terrestrial approaches (Bailey and Omernik ecoregions), and one aquatic approach (Maxwell et al. 1995). The *a posteriori* frameworks included: geographic proximity groupings, non-spatial random groupings, and groupings based on fish community similarity.

Chapter two explored the relative importance of physical vs. ecological boundaries to stream fish dispersal by constructing and testing hybrid ecoregion-by-watershed frameworks using the same CS analysis as above.

To understand the influence of humans on Chapter One and Two results, and to quantify homogenization of stream fish communities, Chapter Three evaluated the change in beta similarity among watershed fish faunas in Kansas before major human modifications to streams (pre-1958) and after modifications (post 1988).

Chapter one showed that the framework based on geographic proximity produced the highest CS values at both scales compared to other classification frameworks.

Chapter two indicated that the hybrid ecoregion-by-watershed frameworks did not effectively classify stream fish communities at the scale tested here.

Chapter three revealed that past watershed faunas in Kansas were more regionally distinct, and have become 8.2% more similar to each other since major stream modifications. Results from both Chapters one and two indicated that geographic proximity is one of the most influential forces on landscape-scale patterns in stream fish communities, which highlights the importance of historical species distributions on modern stream biota.

DEDICATION

I dedicate this book to my Grandma, Dorothy Marie Kennedy, who passed away at the start of my doctoral education, and who always knew how to find joy in togetherness.

I also dedicate this book to my mom and dad, who have loved me and supported my dreams always.

ACKNOWLEDGEMENTS

I would like to thank my family: Rosemary, Barry, Ben and Brett for their support throughout the dissertation writing process. My mom, Dr. Rosemary Chapin, has always said the encouraging things I needed to keep going, and has helped me find the right path in several instances. My dad, Barry Chapin, has kept bringing up the dreaded topic of the dissertation even when he knows this is the last thing I wanted to discuss, and has been a constant source of momentum. Thank you for continuing to bring it up! My grandparents Chapin and Kennedy have also been a source of love during this work

This work would not have been possible without the strong mentoring of my advisor, Dr. Frank “Jerry” deNoyelles. He has been a friend and mentor throughout both my Master’s and Doctoral degrees. Additionally, I would like to thank Dr. Val Smith for his mentoring and his superior editing help with many documents and publications over the years. Dr. Donald Huggins has been integral to producing this work. His Central Plains Center for Bioassessment (within the Kansas Biological Survey) provided the access to agency databases that were used in the analyses for the dissertation. Thanks also are due to my other committee members, Dr. Steven Egbert and Dr. Edward Wiley. Other faculty who I thank include: Dr. Frank Cross; Dr. Jorge Soberon; and Dr. Townsend Peterson.

Many thanks to students and staff of the Kansas Biological Survey. Particularly, I would like to thank: Debbie Baker; Dr. Barbara Haford; Jeff Anderson; Todd Aschenbach; Lisa Castle; Alex Fraser; Erin Questad; Sharon

Ashworth; Kelly Kindscher; Scott Campbell; Carleen Roberts; Andy Dzialowski; and Ed Martenko. The positive working environment provided by the people at the Biosurvey helped me to accomplish my goals.

Thanks also go out to the agencies and their staff (in parentheses) that provided the data and some of the GIS coverages that were used for this dissertation. These include: the United States Environmental Protection Agency Region VII (Robert Barber); Kansas Department of Wildlife and Parks (Kristen Mitchell); Nebraska Department of Environmental Quality (Ken Bazata); the United States Forest Service (Tina Haker); and the Iowa Department of Natural Resources (Tom Wilton).

I would like to acknowledge the following sources of financial support: The Madison and Lila Self Graduate Fellowship; Organization for Tropical Studies Scholarship; Ida Hyde Scholarship; Peace Frogs Scholarship; Knauss Marine Policy Fellowship; Ecology and Evolutionary Biology presenter travel fund; and the Graduate School presenter travel fund.

The Self Fellowship was a valuable experience for me in that it expanded the range of disciplines I was exposed to during my doctoral education compared to the typical doctoral student experience. Thank you Madison and Lila Self!

Thank you so much, Leo Zavarse, for your love and support during this challenging time.

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INTRODUCTION TO THE DISSERTATION

If scientists can describe or quantify the natural range of variation in ecosystem components over space (and time), we can better gauge the human contribution to large scale environmental change such as global warming, extreme weather phenomena, and biotic homogenization through species invasions and extinctions. Quantifying this variation can also elucidate the mechanisms underlying natural shifts in observable ecological realities. One way that scientists are trying to describe natural spatial variation in ecosystems is by creating regional classifications such as ecological regions (ecoregions) based on criteria they deem most important in shaping distinct ecosystems at a coarse scale. Contemporary ecoregions are generally hierarchical and are nested within each other. An ecoregion can be smaller than 700 km^2, as in James Omernik's level IV ecoregions (e.g., the alkaline lakes area within the Sand Hills of Nebraska) or larger than 2 million km^2, as in Omernik's level II ecoregions (e.g., the Great Plains), which are used currently by the U.S. Environmental Protection Agency (Omernik 1995, Chapman et al. 2001). Another well-known ecoregional approach has been published by Robert Bailey (1995) and further developed by Cleland et al. (1997) for the United States Forest Service.

These ecoregion classifications should include environmental characteristics that are influential to lotic systems, because they are being applied to streams by management agencies. Because the valley influences the stream (Hynes 1975), terrestrial criteria are generally used to define these regions of ecological similarity (see Table 1). However, this focus on using terrestrial criteria to create ecoregions also begs for a test of their applicability to aquatic systems. It would seem that more specifically aquatic criteria (i.e., distributions of aquatic biota and substrate composition) would be additionally useful to scientists and natural resource managers for classifying streams. Therefore, the bulk of this dissertation focuses on testing the ecological validity of these ecoregion frameworks for classifying stream systems by looking at the correspondence between ecoregion boundaries and patterns in stream fish community similarity. Stream fish community patterns are employed because they can be used as a surrogate for patterns in stream ecosystem characteristics (e.g., in-stream physical habitat and riparian condition) over the landscape. Additional regional and non-regional classifications for streams (e.g., watersheds) are tested as well to put the ecoregional approaches into context and in order to elucidate the importance of certain large-scale factors that these other classifications incorporate into their design.

Included among these other regional classification approaches is the often-used watershed approach, which is based on the topographic characteristics of the land surrounding a point on a stream (USGS 1982 and Seaber et al. 1987). In addition, the aquatic ecological units (AEU) developed by Maxwell et al. (1995) for the Forest Service represent an intermediate approach in that both terrestrial and aquatic criteria are used to define regions. This classification is based on the Bailey ecoregions, but it more actively incorporates watershed boundaries and zoogeographic features (see table 1). Strahler stream order (Strahler 1964) represents a non-regional classification of streams that is generally seen as a surrogate for discharge and stream size. All of the classification approaches represent different "ready-made," testable hypotheses of the expected organism-environment interactions in streams, because similar ecological systems are generally grouped together by these approaches based on the environmental variables predicted to have the strongest influence on biological communities.

This dissertation includes three studies that explore large-scale patterns in stream fish communities in four states of the Midwest (Kansas, Missouri, Nebraska and Iowa) in order to inform the design of classification systems that are being applied by researchers, conservationists, and managers to streams, and in order to elucidate important mechanisms that shape stream ecosystems in this region.

Chapter One compares the relative applicability of several different classifications for streams in the Midwest using fish community patterns as a surrogate for stream ecosystem characteristics, such as water chemistry (trophic status), in-stream physical habitat, riparian condition and abundance of certain prey species. The extent to which community similarity within groups is greater than community similarity among groups in each classification approach indicates the classification strength (CS) of that approach. In short, the results from the CS analysis inform us as to which classification approach includes large-scale driving forces that are potentially influential to stream ecosystems. Further, the rankings of the classification approaches indicate the relative importance of certain environmental factors as underlying mechanisms that shape large scale patterns in stream fish communities in this part of the Midwest. Researchers, conservationists, managers, and policy makers can use this information to explore these mechanisms, and to further fine-tune the ecoregion approach, in order to more fully account for natural variability in stream systems. This study is unique in that a comparison of different large-scale approaches to classifying streams in this part of the Midwest (KS, MO, NE, IA) has not been done before, although ecoregions have been actively applied to these streams as a management, conservation, and research tool for several years by the USEPA, Kanas Department of Wildlife and Parks, Nebraska Department of Environmental Quality, Iowa Department of natural Resources, etc. Additionally, the extensive database that has been created for this study can be used to identify general patterns in fish community distributions not revealed previously by un-integrated, within-state analyses. The database can also be used by other researchers to ask questions regarding the community ecology of stream fishes over the four-state area beyond the scope of this work.

Chapter two explores the relative importance of physical boundaries to dispersal compared to ecological boundaries to dispersal for stream fish in the Midwest. The information in Chapter One reveals that watershed boundaries (representing physical boundaries to dispersal) and ecoregions (representing ecological boundaries to dispersal) have a similarly high classification strength ranking. This indicates that these different types of dispersal limitations may be equally important in shaping stream fish communities. To test the relative importance of these two types of barriers/influences on fish communities, a hybrid framework is constructed consisting of the two ecoregion approaches mentioned earlier stratified by HUCs (hydrological unit codes – Seaber et al. 1987). The extent to which the hybrid regions outperform (or do not outperform) the unaltered HUC (watershed) and ecoregion classification approaches indicate the effectiveness of putting an equal weight on physical boundaries and ecological boundaries to dispersal in the design of stream classifications for the Midwest. To further understand what may be driving stream community patterns in this region, the same classification strength (CS) analysis used above is performed on a subset of the data, but the fish communities are divided up by functional feeding group rather than species.

Chapter Three addresses homogenization in Midwestern stream fish communities in Kansas. The database and CS analyses made in the preceding chapters indicate that there is much unexplained variation in fish communities, suggesting that there is a random nature to the fish distributions, or that there are aspects of present-day fish distributions that defy fully classifying the steams based upon the classification approaches above. Therefore, it seems that human activities may very well have extirpated and translocated species in such a way that spatial patterns that may have been clear in the past are not detectable. To understand the extent to which human interference is a factor in understanding the results of the previous two studies, and to assess the extent of homogenization that has occurred in stream fish communities of this part of the Midwest, Chapter Three assesses the change in beta similarity of fish communities among watersheds in Kansas before major human modifications to streams (pre-1950) and after human modifications (post 1988). The change in beta similarity between past and present reveals whether regionally distinct communities have become homogenized and the extent to which homogenization has occurred throughout Kansas. At a finer scale, parts of the study area that have been the most altered are identified. Finally, the extent of homogenization is quantified with this analysis and can better-inform us as to the actual historical undisturbed, or reference, conditions in specific regions. This information can serve as a caveat to any assessment of currently-attainable or best-attainable conditions in streams of this part of the Midwest in that we now have knowledge of how different currently attainable conditions are from historic undisturbed stream conditions.

CHAPTER ONE

Regional Patterns in Stream Fish Communities Compared to Ecoregional Boundaries: Does ecoregional location explain variation in stream biota?

Introduction

Characterizing the underlying natural variation in stream systems at a regional scale is important, because it will help in monitoring and research efforts that will detect broad scale environmental change, and it will also provide for attainable region-specific management goals. Further, this macroscopic approach can elucidate underlying mechanisms that shape broad scale patterns in stream communities and can also help to identify regionally specific problems affecting streams (e.g., declining numbers of fish species or homogenization of habitats and communities).

Ecological regions (ecoregions), originally coined by Crowley (1967), represent location-specific hypotheses of expected organism-environment interactions. Ecoregion delineation is an attempt to account for natural spatial variation in ecosystems and their components, such as physical habitat and biota present. Scientists are currently using ecoregions such as those developed by Robert Bailey (1976; 1995; 1996; see also Cleland et al. 1997) and James Omernik (1987; 1995) to classify stream ecosystems into geographic groups that presumably share similar characteristics, such as community composition and water chemistry. This study attempts to assess the utility of these ecoregions for classifying stream systems in the Midwest relative to other approaches that can be used to classify stream types.

These nested hierarchical ecoregion classifications encompass a greater range of scales and employ a broader range of defining criteria than historical efforts to classify areas that share similar natural components; such as efforts by Wallace (1876), Merriam (1894), Sampson (1927), Shelford (1954), Kuchler (1964), Holdridge (1964) and, more recently, the USGS (HUCs or watersheds – 1982) and Seaber et al. (1987). Both Bailey and Omernik used mostly terrestrial characteristics - climate, land form, potential natural vegetation (Kuchler 1964), geology, soil type, and land cover - in their work (also see Table 1). The main difference was that

Omernik gave more emphasis to landcover (accounting for the influence of humans), while Bailey relied most heavily on climate (energy inputs) to define his ecoregions. Also, Omernik's regional scheme was designed from inception to be applied to aquatic systems, although it incorporates no specifically aquatic criteria. Various classification efforts have followed; many with the aim of ecosystem and species conservation (Dinerstein et al. 1995, Ricketts et al. 1999, Abel et al. 2000) in both terrestrial and aquatic environments. These classification approaches are often based on the concept of the ecoregion as developed by Bailey and Omernik.

Many agencies and researchers use the ecoregion classification to shape their research questions and structure their monitoring efforts. The USEPA has developed and uses Omernik ecoregions (Gallant et al. 1989, Omernik 1995), while the USFS has supported development and application of the Bailey ecoregions (Bailey 1995 and Cleland et al. 1997), and uses the Bailey technique as a basis for a classification approach that integrates watershed boundaries and aquatic zoogeography into its design (the aquatic ecological units of Maxwell et al. 1995). The Bailey approach has also been used as the basis for The Nature Conservancy's classification of aquatic habitats as well as the World Wildlife Fund's freshwater ecoregions of North America (Abel et al. 2000).

Even though ecoregions are widely applied, there are still many unresolved issues that make their application to streams potentially problematic. Listed below are three major issues addressed in this study. First of all, there is disagreement as to the utility of terrestrially defined ecoregions (i.e., Omernik 1995 and Bailey 1996) versus aquatically defined regional schemes (Maxwell et al. 1995 and Abel et al. 2000) in the classification of stream systems. The more terrestrially based classifications may be criticized because they do not specifically and consistently incorporate the parameters that are unique to water bodies (e.g. distributions of aquatic biota; differences in watershed boundaries; and changes in in-stream physical habitat). In response to this, Maxwell et al. (1995) recommend that a combination of both a terrestrially-based and an aquatically-based classification should be used to circumscribe regions of similar aquatic systems. However, this approach may not be practical, because the application of both a terrestrial and an aquatic classification in delineating regions may be so cumbersome as to be useless.

A second issue regarding regional classifications for streams is that the relative utility of applying HUCs/watersheds (representing *physical* boundaries to species dispersal) vs. ecoregions (representing *ecological* boundaries to dispersal) in different regions is not well-studied. This is dealt with here initially, but is further explored to a greater extent in Chapter Two.

Thirdly, the relative utility of the different classifications being employed by managers, scientists and conservationists for streams has not been addressed in large areas of the Midwest. It is important to identify the classification approaches that work best or worst specifically for Midwestern streams. Additionally, the classification approaches represent ready-made, testable hypotheses about the relative importance of environmental parameters such as climate, landuse or soil type to stream systems. By undertaking a comparison of the relative utility of several classification approaches, which emphasize different suites of environmental factors when classifying streams, important large-scale mechanisms influencing patterns in stream fish communities could be elucidated.

This study addresses the issues described in the preceding paragraphs by comparing the correspondence of various classification approaches (representing different hypotheses of the organism-environment interaction) with observed stream fish community patterns in four states of the Midwest (KS, NE, IA, MO). This involves calculating a classification strength (CS) for each classification approach based on the difference between mean similarity of fish communities within groups and mean similarity of fish communities among groups. A classification is deemed stronger (and more applicable to streams) the greater the mean similarity between fish communities within the same groups is relative to the mean similarity between fish communities among different groups in that classification.

The classifications being compared here include four *a priori* and three *a posteriori* approaches that are both regional and non-regional in nature (see Table 1). The *a priori* classification approaches include the two more terrestrially-based (1) Bailey (Cleland et al. 1997) and (2) Omernik (1995) ecoregions; (3) the aquatic ecological units of Maxwell et al. (1995); and (4) the watershed-based HUCs of the USGS (1982) (see figures 1 through 4). The *a posteriori* classification approaches that will be compared to the above approaches include: (1) a non-spatial design (a random assignment of sites to groups) that represents the assumption that there is no class structure to the stream fish communities and will give the lowest possible classification strength value; (2) a hydrologically and ecologically neutral spatial design based only on intersite geographic distance clusters; and (3) a classification based on clusters of taxonomically similar sites (taxonomic fish clusters), which represents the maximum attainable classification strength. The inclusion of the taxonomic fish clusters and the randomized design are after Van Sickle and Hughes (2000).

This study makes a significant contribution to landscape level stream ecology in that a comparison of the utility of different large-scale approaches to classifying streams in this part of the Midwest (KS, MO, NE, IA) has not been done before, although ecoregions have been actively applied to these streams as a management, conservation, and research tool for several years by the USEPA, Kansas Department of Wildlife and Parks, Nebraska Department of Environmental Quality, Iowa Department of Natural Resources and other organizations.

Materials and Methods

Experimental design and classifications analyzed

The study area spans most of Nebraska, Kansas, Iowa and Missouri. This was a bioinformatics-based study that utilized disparate databases from government agencies across the extensive study area to test the ecological validity, or classification strength (CS), of regional classification approaches for streams in the

Midwest. The methods employed here were designed to allow comparison with a study by Van Sickle and Hughes (2000). Van Sickle and Hughes' article laid out methods for studies done for the Journal of the North American Benthological Society's 2000 publication entitled "Landscape Classifications: Aquatic Biota and Bioassessments," which indicated a lack of research comparing the applicability of current regional classification approaches to Midwestern streams.

The classification strengths of four *a priori* regional classification approaches were assessed in regards to their ability to classify stream fish communities (see below for a description of the CS calculation). Both larger and smaller regional subdivisions were assessed for each of these hierarchical classifications for a total of eight CS calculations. The *a priori* regional classifications included: 2-digit (larger) and 4-digit (smaller) Hydrologic Unit Codes (HUCs); provinces and sections of Bailey's ecoregions; levels II and III of Omernik's ecoregions; and subregions and river basins from Maxwell et al. These all represent comparable scales (see Table 1 and Fig.s 1-4).

To put these four classification approaches in context, they were compared to three non-regional classifications: the *a priori* Strahler stream order (a surrogate for stream size and discharge); an *a posteriori* random assignment of sites to groups (to represent the minimum possible CS and to evaluate the hypothesis that there is "no class structure" to stream communities); and taxonomic fish clusters based on a fish community cluster analysis that produced *a posteriori* groups of the most similar fish communities that represented the maximum attainable CS for the classifications. In order to look at the effect of proximity (spatial autocorrelation) on fish community patterns, a classification was included based only on the physical distance between stream sites (geographic distance clusters). Because the geographic distance clusters were grouped based on geographic closeness only, this classification approach was considered hydrologically and ecologically neutral.

Only fish from wadeable reference streams (as identified by the Kansas Biological Survey (KBS), USEPA Region VII, and the Kansas Department of Wildlife and Parks (KDWP)) were included in the study. These are generally streams that are between 1st and 3rd order, but may include 4th and 5th order streams with lower flow. Reference streams (see below for definition) were used in order to mitigate as much of the effect of humans on natural patterns in communities as possible.

Samples utilized in this study were taken by the contributing agencies from 1988 through 2001. The majority of samples were taken from 1994 through 1997. Initially, a survey was sent out to several state agencies to see what kind of stream species and habitat data were available. Based on the survey, fish were chosen as the most widely and consistently sampled taxonomic group (instead of invertebrates) over the four-state region. Through my association with the KBS and Dr. Don Huggins, data was requested and received from the Nebraska Department of Environmental Quality (NDEQ), the Missouri Department of Natural Resources (MoDNR), the USEPA Region VII, the Iowa Deparment of Natural Resources (IDNR), and the Kansas Department of Wildlife and Parks.

Fish communities were used as representatives of the stream ecosystem because their whole life is spent in water, they are relatively long-lived so they are integrative of historical and current impacts in streams, and they are used as bio-indicators of ecosystem health and biotic integrity (Karr 1981). Another advantage to using a biological component like fish to represent the reference stream ecosystem is that, based on analyses of 1994 and 1995 REMAP (Regional Environmental Monitoring and Assessment Program) data, many biotic characteristics such as Index of Biotic Integrity (IBI) scores and % of nonnative fish individuals differed significantly ($\rho \leq 0.05$) among reference (least disturbed) vs. non-reference (randomly selected) streams based on parametric (independent t-test) and nonparametric (independent Wilcoxon) statistical tests. However, most physical habitat and chemical characteristics did not differ significantly (Chapin unpublished data). Also, fish are similarly sampled across agencies and state boundaries (unlike invertebrates), so the data sets are comparable.

The sampling protocol for stream fish was based on procedures from the USEPA (Plafkin et al. 1989, Paulsen et al. 1991, and Barbour et al. 1999). Fish were quantitatively sampled using DC pulse electrofishing and additional seining in all states except Iowa, where only electrofishing was performed. The reach length sampled was 40 times the mean wetted width of the channel.

Classification strength calculation

Fish community similarity indices were used to calculate a classification strength (CS) for the various regional and non-regional classifications being tested (after Vansickle and Hughes 2000) and included: the Sørensen (richness) index (Sørensen 1948) and the Bray-Curtis (relative abundance) index (Bray and Curtis 1957). After culling the data, a master matrix of 231 sites by 142 species was loaded into PC-ORD for Windows (version 4.20, 1999, MjM software, Gleneden Beach, Oregon), and a matrix of dissimilarities (1- similarity) among each pair of sites was generated for both indices (see Table 2 for a partial similarity matrix of sites).

The Sørensen index (S.I.) is as follows:

$$\text{S.I.} = 2c/(s_1+s_2) \qquad \text{Eq. 1}$$

Where s_1 is the number of species in community 1; s_2 is the number of species in community 2; c is the number of species both communities have in common.

The Bray-Curtis index (B.C.I.) is as follows:

$$\text{B.C. I.} = \left(\frac{1}{P}\right) \frac{\Sigma\ |X_{ik} - X_{jk}|}{\Sigma\ (X_{\underline{ik}} + X_{\underline{jk}})} \qquad \text{Eq. 2}$$

Where X_{ik} is the number of individuals of species k at site i; X_{jk} is the number of individuals of species k at site j; P is the number of total species at both sites combined.

Pair-wise iterative comparisons were used to calculate the relative similarity of stream communities within groups vs stream communities among groups. The variables calculated for each classification scheme were: Mean similarity of sites within a group (W_i); Overall weighted mean similarity of sites within groups (W); Mean similarity of sites among groups (B); and classification strength (CS = W-B with values of -1 to 1). The overall weighted mean similarity of sites within groups (W) was calculated according to Van Sickle and Hughes (2000):

$$W = \Sigma_i(n_i/N)W_i\,, \qquad \text{Eq. 3}$$

where n_i is the number of sites in group i and N is the total number of sites in all groups. The classification is judged to be stronger if the within group similarity (W) is much higher than the among group similarity (B) of fish communities.

The variables above were calculated using the MRPP (Multiresponse Permutation Procedures) analysis within PC_ORD (version 4.20, 1999, MjM software, Gleneden Beach, Oregon) and the MRPP extension (MRPPCONV.exe). The extension is part of the newest version of the Meansim 6 software package developed by Van Sickle and Hughes (2000) and available from the EPA's Western Ecology Division website

(http://www.epa.gov/wed/pages/models/dendro/mean_similarity_analysis.htm).

The output from the Meansim 6 software includes the *p*-value for the randomization test, which randomly assigns stream sites iteratively (ten thousand times) to the same number of groups as in the classification approach being tested. Then, the average CS from the randomly constructed groups is compared to the CS for the classification approach being tested. A low *p*-value ($p<0.001$) is attained if the average CS from the 10,000 random trials is significantly less than that obtained by the classification approach being evaluated. This indicates that there is some sort of "class structure" in the stream communities.

Small and large geographic distance clusters were created for comparison with the smaller and larger nested subregions within the classifications. To create the small clusters, 8 geographic distance clusters of comparable size to the regional frameworks were constructed. A grid with 8 sections was then overlain on the study area, and the nodes of the clusters were randomly selected from each section. The grid was constructed with enough buffer distance between sections so there would not be overlapping points in the different clusters. The "select by theme" feature was used in ESRI's ArcView GIS software (Environmental Systems Research Institute, Redland, USA) to select sites that were at most 150 km from the nodes to give eight amorphous, non-overlapping regions of roughly similar size to the *a priori* regional frameworks. Large clusters were constructed in a similar fashion, but a 300 km radius was designated around each randomly chosen node in four distinct sections of the study area to construct four large distance clusters (see Fig.s 5 and 6 for the smaller and larger geographic distance clusters).

The taxonomic fish clusters (representing the maximum CS attainable) were constructed based on the flexible β cluster analysis (β=-0.1) following the methods of Lance and Williams (1967), Legendre and Legendre (1983) and Belbin et al. (1992). Resulting dendrograms were pruned to equal the number of groups in the classification being tested. The performance of each of the classifications relative to their maximum attainable CS (% of the maximum attainable CS) could then be compared.

As a way to graphically compare the classification strengths (CS) of several classifications and the similarities of fish communities within distinct groups or regions, similarity dendrograms were constructed. The base or node of the dendrogram is equal to the mean similarity of sites among groups (B) in a classification, and the length of a branch is equal to the mean within group similarity (W_i). The number of branches on the dendrogram is equal to the number of groups within the classification being tested.

Data culling and database manipulation

The databases were extensively reformatted and merged to create a site by species matrix. The names for fish species were recoded to be consistent across databases following the style of the Regional Environmental Monitoring and Assessment Program (REMAP) for EPA region VII. Through extensive quality checking, synonymous, outdated, or misspelled species names were identified and corrected, and new codes were assigned to the sites so they would be compatible with the software used in the analyses (see below). The final matrix contained 231 reference sites by 142 species. The final sites were culled from original datasets containing over a thousand candidate sites.

Data were culled to avoid drought and flood years based on the Palmer index of drought severity (Palmer 1965) so that sporadic, temporary species absences or appearances due to these conditions could be avoided. Palmer index values were taken from the National Oceanic and Atmospheric Administration's National Climatic Data Center (NCDC) website

(http://www.cdc.noaa.gov/USclimate/).

Mild to severe drought (Palmer values of –1.0 to –6.0) was found to cover most of the study area in 1989, 2000 and 2002. Therefore, those data-years were generally excluded from the study. 1993 data were excluded due to widespread flooding throughout the study area. Rarely, data from the above years were included if the stream site in question was not sampled during any other year.

The original data set contained sites that were sampled multiple times per year and over multiple years. Because of this, these data were further culled to only include one sample per site so temporal variation at a site would not interfere as much with the detection of spatial variation. In a geographic information system (GIS) environment (ESRI's ArcView 3.3 software), sites that were 5 miles apart or closer on a stream reach and were not separated by a confluence point were judged to be from the same site, and the data from one of the sites was omitted so as not to skew the classification strength analysis. Individual fish records were deleted from any stream sample that were not confirmed identifications of a species (i.e., they had a "?" next to the record), or if the fish were hybrids, as long as the unidentified or hybrid individuals made up 5% or less of the total individuals in a community. If unidentified fish species made up more than 5% of a community, the entire stream record was deleted from the analysis. This happened only with some sites in the KDWP dataset.

These data were brought into a GIS (ESRI's ArcView 3.3 software) and projected onto maps (coverages or themes) depicting the various regional classifications being tested in order to assign sampling points to correct regions and envision the spatial spread of the sites. Coverages of the different regional classifications were obtained from Tina Haker at the USDA-Forest Service (HUCs based on Seaber et al. 1987, and the aquatic ecological units of Maxwell et al. 1995), from the US Forest Service website (Bailey's ecoregions - http://www.fs.fed.us/institute/ecolink.html) and from the USEPA's Western Ecology Division Website (Omernik's ecoregions - http://www.epa.gov/wed/models/ecoregions.htm – 2004). The polygon (region) and point (site) coverages were reprojected to the Albers equal area projection (reference latitude of 37.5 degrees) to look at spatial overlap between the frameworks and to eventually create hybrid regions (see Chapter two and Fig.s 1 through 4).

Results

Rankings of the Classifications

This study used patterns of similarity in fish communities to test the relative classification strength (CS), or ecological validity, of several approaches to classifying stream systems in Kansas, Missouri, Nebraska and Iowa. The CS rankings will inform scientists and managers as to the utility of these classification approaches in accounting for natural spatial variation in least-disturbed, or reference, stream ecosystems in this part of the Midwest.

Each of the non-regional and regional classifications (at both coarser and finer scales) performed better (i.e., had a higher classification strength) than a random reassignment of sites to groups based on the permutation tests ($p<<0.000001$), no matter whether the Bray-Curtis or the Sørensen index was used. The classification strength (CS) values for the finer-scale regional classifications (analogous to Omernik level III ecoregions) ranged from 0.16 to 0.2 (Sørensen analysis) and from 0.09 to 0.11 (Bray-Curtis analysis) out of a theoretical maximum CS of 1. These CS values were expressed in this study as percentages of 1 (i.e., 16%, 20%, 9% and 11% respectively: See Table 3).

The taxonomic fish cluster analyses were used to estimate the maximum attainable CS for the classifications in order to calibrate their CS values. At the finer-scale, the maximum attainable CS values ranged from 23% to 26% for the Sørensen analysis and from 17% to 21% for the Bray-Curtis analysis (see Tables A and B in the appendix). A comparison of the % of the maximum attainable CS (hereafter referred to as the % of the maximum CS) that a classification achieved was then possible based on the above CS values for the taxonomic clusters, and we see that among the finer-scale classifications the % of the maximum CS ranged from 69% to 79% for the Sørensen analysis and from 43% to 57% for the Bray-Curtis analysis (see Table 3).

The CS for the Strahler non-regional orders and the coarser-scale regional classifications (analogous to Omerik level II ecoregions) ranged from 7% to 15% based on Sørensen similarities (see Table 4, which includes other results for the coarser-scale subdivisions).

Rankings of the classification strengths (CS) for the finer-scale divisions came out differently depending on whether presence/absence data or abundance fish data were used (see Table 5). Based on the Sørensen similarities (presence/absence data), the geographic distance clusters (with 79% of the maximum CS) were most predictive of areas where similar fish communities would occur (Table 3 and Table 5). Both the Omernik framework and the Bailey framework performed equally well in second place with 75% of the maximum CS, and were followed by 4-digit HUCs (73%), Maxwell's River Basins (69%) and Strahler stream order (30% of the maximum CS). Based on the Bray-Curtis similarities (relative abundance data), the Omernik framework performed best (57% of the maximum CS), followed closely by the Bailey framework (55%), Maxwell River Basins (50%), 4-digit HUCs (48%), geographic distance clusters (43%), and finally stream order (27%). Maxwell's river basins did much better based on abundances rather than presence/absence data, while geographic distance clusters performed distinctly better when tested using presence/absence data. Omernik's and Bailey's ecoregions generally came out with a similarly high % of maximum CS relative to other frameworks using both presence/absence and abundance data, but the Omernik framework was somewhat more reflective of shifts in relative abundances among regions than the Bailey framework.

For the larger divisions, the CS rankings seemed slightly less dependent on whether presence/absence data or abundance data were used. The rankings of the classification strengths contrasted with the results from the finer divisions. Maxwell's Subregions and the large Geographic Distance Clusters were the most reflective of fish community patterns at this coarser scale, with 83% and 82% of the maximum CS value respectively based on Sørensen similarities (Table 4). The next highest CS values based on the Sørensen analysis were Omernik Level II ecoregions (70% of the maximum CS) followed by Bailey's Provinces (63%), 2-digit HUCs (55%) and finally Strahler Order (30%). Based on Bray-Curtis similarities, Maxwell's Subregions and the Geographic Distance Clusters again both did much better than the other classifications (both with 69% of the Maximum CS). These classifications were followed by the 2-digit HUCS (61%), the Omernik Level II ecoregions (60%), Bailey's Provinces (47%) and Strahler Stream Order (27%).

Trends in the % of the Maximum CS at different scales

The average % of the maximum CS based on Sørensen similarities decreased from 74.3% for the finer regional divisions to 70.6% for the larger regional divisions (Table 6). The HUCs' maximum CS decreased the most (by 18%) when moving from finer (4-digit) to coarser (2-digit) subdivisions. Alternatively, the Maxwell framework and Geographic distance clusters increased their % of the maximum CS when larger subdivisions were employed (14% and 3% increases respectively).

In contrast to the trends resulting from presence/absence data, the average % of maximum attainable CS increased from 50.6% for the finer divisions to 61.4% for the larger divisions when using Bray-Curtis similarities (relative abundance data). The Maxwell Subregions and large Geographic distance clusters increased the most when moving from finer to larger subdivisions (a 19% and 26% increase in the % maximum CS respectively). The Bailey Provinces were the exception to this trend, with an 8% decrease in the % maximum CS. Finally, the average CS based on the taxonomic fish clusters dropped substantially for both similarity indices when moving from finer to larger subdivisions (or, in orther words, from more taxonomic clusters to fewer, larger clusters) (see Tables A and B in the appendix).

Similarity dendrograms and the CS of individual groups within a classification

The classification strength (CS) of an individual group or region within a classification can be calculated as the within-group mean similarity of stream sites minus the overall mean similarity among groups (W_i-B) and put into graphical format by constructing a similarity dendrogram. Figures 7 and 8 show Sørensen and Bray-Curtis similarity dendrograms for six classifications (at the finer scale) being tested with this work. The longest branch in the dendrogram indicates the region or group that has the highest individual CS (Wi-B) or the most unique fish assemblage compared to other regions in the classification (see starred branches in the dendrograms). The group that had the highest individual CS was the Omernik Flint Hills ecoregion for both the Sørensen and the Bray-Curtis analyses. Also for both similarity analyses, the Niobrara 4-digit HUC had the lowest individual CS of all the groups. If most of the branches are of a similar length, then the classification does an equally effective job of dividing up streams into groups containing similar communities throughout the study area. The node or base of the dendrogram is equal to the overall mean similarity among groups (B) in a classification. If the fish communities among groups have a high similarity (i.e., the B value is higher than for other classifications), the classification is most likely not as applicable to streams.

Generally, the geographic groups with the longest branches (highest individual CS) fell within the south central part of the study area (the Flint Hills area in east/central Kansas) and the northeastern part of the study area (the glaciated areas of central and northeastern Iowa) (see starred regions on Fig.s 1 through 5).

However, an area that is just east of the center of the study area (roughly coinciding with the Missouri-Nishnabotna basin) performed best based on the HUC and the Maxwell dendrograms constructed from Sørensen similarities (see Fig.s 3 and 4). In the stream order analysis, the fifth order streams had the highest individual CS. The groups that usually performed worst (had the lowest individual CS values) across all classifications were located in the western high plains of Nebraska and Kansas and the Nebraska Sand Hills area (see labelled regions in Fig.s 1 through 5). The third order streams performed worst in the stream order analysis. Of course, the non-geographic taxonomic fish clusters were the best-performing classifications with the highest individual CS values because of the nature of their construction (dendrograms not shown).

The taxonomic fish clusters were projected onto the map of the study area to assess whether the sites from the same clusters clumped together geographically. They were also projected onto the various regional classification schemes at the finer scale to give a visual idea of whether there was correspondence between the regional boundaries and the fish clusters (Fig.s A through D in the appendix). The Sørensen fish clusters (Fig. 9) were more tightly clumped than the Bray-Curtis fish clusters (Fig. E in the appendix) and showed four or five distinct fish regions (see circled areas on Fig. 9); one cluster (cluster 25) covered most of Iowa (excluding the Southwestern portion) and had a community generally composed of the sand shiner (*Notropis stramineus)*, the Johnny darter (*Etheostoma nigrum)*, white sucker (*Catostomus commersoni)*, bluntnose minnow (*Pimephales notatus*) and creek chub

(*Semotilus atromaculatus*); a second cluster (cluster 3) in the southern half of Missouri characterized by the widespread presence of slender madtom (*Noturus exilis*), smallmouth bass (*Micropterus dolomieu*), blue gill (*Lepomis macrochirus*), long-eared sunfish (*Lepomis megalotus*), Ozark minnow (*Notropis nubilus*), green sunfish (*Lepomis cyanellus*), central stoneroller (*Campostoma anomalum*) and largescale stoneroller (*Camposoma oligolepis*); a third cluster (cluster 9) in the eastern third of Kansas, which had a community composed mostly of the orangethroat darter (*Etheostoma spectabile*), red shiner (*Cyprinella lutrensis*), largemouth bass (*Micropterus salmoides*), central stoneroller, green sunfish and bluntnose minnow; a fourth cluster (cluster 6) mostly in the south central portion of Kansas composed mainly of the fathead minnow (*Pimephales promelas*), common carp (*Cyprinus carpio*), channel catfish (*Ictalurus punctatus*), green sunfish, sand shiner and red shiner; and a fifth, more diffuse, cluster (cluster 1) mostly in the center of the study area spanning the Nebraska and Iowa borders and running west across Nebraska characterized by the the presence of bigmouth shiner (*Notropis dorsalis*), creek chub, green sunfish, sand shiner and fathead minnow.

There was generally not much correspondence between the regions in the geographic classifications being tested here and the taxonomic fish regions that were generated from the cluster analysis.

The characteristic fish assemblage in each ecoregion

To identify what species assemblage is characteristic of a typical reference stream in a region, ranked occupancy tables were created based on the number of streams a species occupies within the area of interest. Table C in the appendix lists the species from the highest to the lowest percentage of streams occupied in a region. This analysis ranks the species based on how widespread it is, rather than ranking the number of individuals per species present in a region. We can assume that the species with the top percentages of occurrence overlap greatly and make up the communities found throughout most of the region of interest.

Tables 7 and 8 were constructed from the information in Table C. Tables 7 and 8 list the widespread and unique species that characterize the different Omernik level III ecoregions that were analyzed in this study. Species were categorized as: widespread (the species occupies at least 70% of the streams surveyed in an ecoregion); widespread and distinctive (meaning they are only widespread within this ecoregion, but still may occur in other ecoregions studied here), unique (the species is only found in one ecoregion); and rare but somewhat restricted (the species occurs in one ecoregion in a few streams, but also occurs in at most two streams outside that ecoregion). A description of the communities that characterize the individual regions is included in the appendix.

Valuable basic statistics about regional fish communities in reference streams can also now be produced for the first time from the database that has been generated by this work. Table 9 gives general ecological information about reference stream fish communities in the four-state study area and in Omernik level III ecoregions such as richness, density and evenness scores. In all, 142 fish species were found in the 231 reference streams that were included in this study (see Table D in the appendix for a list of the fish species that were present in the streams studied here). The basic ecological information found in Table 9 can be very useful in future research attempting to put the Midwest's stream fish communities into context relative to other regions of North America.

Discussion

Overall strength and utility of the classifications

All of the classifications had a higher classification strength (CS) than a random reassignment of stream sites to groups ($p<<.0001$), meaning that they had some value in classifying stream fish communities, and that the hypothesis of no-class-structure for stream communities is rejected. This indicates that all classifications incorporated environmental criteria that were at least somewhat related to stream community patterns in the Midwest.

Based on the taxonomic fish clusters, the Maximum Attainable raw CS value was 26%. Therefore, the taxonomic cluster analysis does not reveal an inherent strong taxonomic similarity among communities at the scales analyzed here. Subsequently, a substantial amount of variation in fish communities is not accounted for using the community similarity indices employed.

In contrast to the low raw classification strength (CS) values, the mean % of the Maximum Attainable CS achieved across all classifications was 74% (Table 6 – finer scale Sørensen analysis). The mean was similar for just the ecoregional classifications (73%) as well. Further, these mean CS values came out 20% lower using the more ecologically informative Bray-Curtis community index (Table 6). These results indicate that the ecoregion classifications are useful – that they do include criteria that account for variation in fish community patterns - especially based on species presence/absence. However, the results also indicate that there is still substantial variation unaccounted for by the classifications tested here – especially related to the realized niche of a species/assemblage as revealed by patterns in abundance. Obviously, there are aspects of the ecoregion delineation process that could be altered to include additional features that have an impact on streams. Some ways to improve the stream classifications are suggested by the results of this study and are discussed below.

The performance of classifications based on scale and community index

From the data in Tables 3 and 4, it is apparent that the spatial scale of comparison and the similarity index used to compare the communities had a definite impact on the correspondence between fish community patterns and the classifications (as measured by the % maximum CS rankings). The Maxwell and geographic cluster classifications performed much better relative to the other classifications at the coarser scale no matter which similarity index was used. At the finer scale, the use of the more ecologically informative Bray-Curtis relative abundance index seemed to favor the ecoregion classifications from Bailey and Omernik over other classifications. Alternatively, the use of presence-absence data (Sørensen index) favored the geographic distance clusters (though slightly) over the ecoregions classifications at the finer scale.

The geographic clusters were the only classification to show a superior correspondence with patterns in fish communities across both spatial scales assessed in this study. This indicates that there is a high degree of spatial autocorrelation in the fish communities in this part of the Midwest. Likewise, in the Mid-Atlantic U.S., McCormick et al. (2000) showed that similarity among fish communities declined with increasing distance. Further, Van Sickle and Hughes (2000) found that a geographic classification based on distance corresponded with patterns in fish communities much better than other *a priori* classifications they tested in Oregon. In Alaska, Oswood et al. (2000) found that fish community similarities between ecoregions were related to the distance in stream miles between two sampling points and, therefore, were likely related to dispersal ability.

On the other hand, this outcome may have been exaggerated by the structure of the geographic clusters, because they were more compact and had fewer sites per group or cluster relative to the other classifications – particularly at the finer scale (see Fig.s 1-6). Also, the construction and subsequent testing of multiple versions of the geographic clusters was not possible because there are few alternative ways to break up the land mass into an equal number of roughly equal-area parcels that contain enough data points for comparison.

Physical boundaries to dispersal vs. ecological boundaries to dispersal (watersheds vs ecoregions)

The analysis using the Sørensen presence/absence index revealed that the ecoregions of Bailey and Omernik were only slightly better at classifying stream ecosystem types than the 4-digit HUCs/watersheds based on the % of maximum CS values. These results suggest that physical boundaries to species dispersal may be having an impact on stream biota that is nearly as important as the suite of strictly ecological factors that are represented in the ecoregions frameworks. On the other hand, the analysis based on the Bray-Curtis relative abundance similarities did not reveal such equally high rankings for the HUC classification. Work described in Chapter Two tested the ecoregion frameworks stratified by HUCs to see if this new hybrid classification would have stronger predictive powers for stream communities in this part of the Midwest. Somewhat similar manipulations and analyses have been attempted in other regions with equivocal results (Van Sickle and Hughes 2000; Feminella 2000).

Comparison of ecological classifications reveals the relative importance of regional environmental factors

The classification strength (CS) comparison performed here elucidates the relative importance of environmental factors emphasized in the different ecoregion classifications (Bailey's, Omernik's and Maxwell's). Based on the relative abundance data, the Omernik ecoregions outperformed all other classifications at the finer scale, but performed only slightly better than the Bailey ecoregions (Table 3). Because the Bailey and Omernik ecoregional frameworks were almost equally predictive of fish patterns in the study area, there does not seem to be an advantage to the increased emphasis placed on climate in the Bailey scheme nor land use in the Omernik scheme as factors strongly influencing patterns in stream biota. Alternatively, this similar performance could be interpreted to mean that contemporary human land use may be equally important as climate in shaping stream communities.

However, closer evaluation of the specific area where the ecoregion frameworks' borders differ most (i.e., the area including the state of Iowa, the northern part of Missouri and far eastern Kansas – see Fig.s 1 and 2) may yield a greater difference in the performance of the two classifications. The Omernik scheme divides this area into 4 regions; the western Cornbelt Plains, the Central Irregular Plains, the Interior River Lowland and the Driftless Area . The Bailey classification divides the area into 5 regions with very different shapes and sizes; the Central Dissected Till Plains, the Osage Plains, the North-Central Glaciated Plains, the

Minnesota and Northeastern Iowa Morainal Oak-Savannah section and the North central U.S. Driftless and Escarpment section.

A comparison of the individual CS values for the regions that make up this northeastern portion of the study area can be used to reveal which classification is more applicable to stream systems there. The average individual CS values for the Bailey ecoregions that occupy this area were higher using both the Bray-Curtis and Sørensen analyses (12% and 20.2% respectively – data not shown) than the average individual CS values for the Omernik ecoregions (10.4% and 18.3% respectively). This is likely due to the fact that the influence of glacial activity is given more weight in the Bailey ecoregion delineation approach in this particular area than in the Omernik approach. It seems that past glacial activity may have a more important influence on fish communities and stream systems in this geographic area relative to present-day land-use. This outcome may point to a greater importance of substrate composition in shaping stream communities and ecosystems because glacial activity greatly influences the distribution of soil types where it has occurred recently on a geological time scale. Additionally, this result may be due to the great impact of isolation on fish communities in glacial refugia and subsequent recolonization patterns in this area. The Omernik approach would likely benefit from a stronger consideration of glacial influences during further ecoregion delineation attempts in this and other glacially impacted areas if the purpose for an ecoregion delineation is to account for variation in stream ecosystems.

The fact that Maxwell's classification did not perform as well as all regional classifications at the finer scale based on the Sørensen analysis, and not as well as the other ecoregions classifications based on the Bray-Curtis analysis is surprising, because it is the only framework of the three ecoregional frameworks that incorporates watersheds and aquatic zoogeographic regions into its design. However, this poor performance could be due to the fact that Maxwell's river basins across Nebraska and Kansas are large and run for great distances laterally, therefore encompassing a steep gradient in moisture from East to West. Also, this result may indicate that specifically aquatic criteria are not as useful as the suite of terrestrial and climate criteria assumed by the other classifications to shape regional patterns in stream ecosystems in the Midwest. It seems that, at least according to fish communities, the Maxwell classification's greater emphasis on aquatic criteria may not be very effective in accounting for variation in stream systems in this part of the country at the finer scale used in this study.

The poor performance of the Stream Order classification

The non-regional Strahler stream orders classified the streams poorly. Therefore, longitudinal location of a stream in a stream network, stream size and discharge do not seem as important as ecoregion location to landscape-scale fish community patterns within the area studied here. Perhaps there is a high degree of endemicity within regions in the study area, which might account for this finding. It must be kept in mind, however, that the assignation of stream order has not been fully completed for the streams evaluated in this study, and only 115 streams could be included in the CS analysis for the orders, compared to nearly double that number for the analysis of the regional classifications. Additional ground-truthing and the use of geo-spatial tools to assign stream order are needed on the part of the state agencies that have been compiling extensive stream data in order to conduct further hypothesis testing on the strength of the relationship between stream order and such things as fish community characteristics in this part of the Midwest.

Lessons learned from comparisons with other studies

As mentioned above, this study was designed so it could be compared to results from a special issue of the Journal of the North American Benthological Society (Van Sickle and Hughes 2000). This issue was devoted to evaluating the utility of landscape classifications in stream bioassessment by looking at landscape level patterns in aquatic invertebrates, vertebrates, and diatoms - mostly in northern or coastal regions. Most of the studies in the journal found that a statistically significant amount of variation in fish, amphibian, or invertebrate communities was explained using regional classifications such as Bailey's and Omernik's, but that the strength of these classifications (especially for invertebrates) was usually weak (Hawkins et al. 2000). Hawkins et al. (2000) emphasized that the type of analyses employed in these studies to assess stream classification strength (CS) should be used in other (southern or central) geographic areas in the U.S.

After surveying the results from the September 2000 publication cited above, this study, and other work, it seems that the ecoregion approaches studied here may be distinctly more appropriate for streams in certain geographic locations than for others. For example, the results of the CS analyses were very different from those produced by McCormick et al. (2000) in the Mid-Atlantic Highlands in which the CS value for the Omernik ecoregions was smaller than that found in this study by a factor of 10 for the Bray-Curtis analysis at the finer scale, and the Strahler orders had the highest CS values of any of the classifications tested. In this study, stream order performed most poorly, just as in the study by Van Sickle and Hughes. CS values (not % maximum CS) found by Van Sickle and Hughes (2000) based on Oregon fish and amphibian assemblages in Omernik ecoregions were the same as that found here for the Bray-Curtis analysis (11%), but were lower for the Sørensen analysis (13% vs 18% CS). However, Van Sickle and Hughes suggested that the moderately strong performance of the ecoregions was due to spatial autocorrelation rather than ecological realities, because of the equally superior performance of a classification they constructed based on geographic proximity. These studies did not calculate the % of the maximum CS, therefore only raw CS values were compared here.

Also in Oregon, ecoregions (as defined by Omernik 1987) corresponded well with ichthyogeographic regions in a detrended correspondence analysis (DCA; Hughes et al. 1987) and with patterns in fish distributions, physical stream habitat and water quality based on DCA and a variety of other multivariate analyses (Whittier et al. 1988). Rabeni and Doisey (2000), the only researchers who have done an ecoregion stream classification strength (CS) analysis in the Midwest (MO), found that variation in stream macroinvertebrate communities matched quite well with ecoregions in Missouri at the finer scale used in this study (analogous to Omernik ecoregion level III). The same result was found for fish presence/absence in this study. At a finer scale than any analyzed here, Rabeni and Doisey (2000) found that the Bailey ecoregion classification was stronger than Pfleiger's 1989 classification (based on fish faunal regions) for aquatic invertebrates, but did not include the Omernik classification in this finer scale analysis. Unfortunately, the researchers did not report raw CS values and did not perform their analyses at a coarser scale (i.e., Omernik level II ecoregions), which hinders comparison with this study somewhat.

In Arkansas, Rohm et al. (1987) found that correspondence was good between Omernik ecoregions (1987) and fish distributions, water quality and physical habitat based on ordination analyses. However, Lyons (1989) used DCA to look at correspondence between Omernik's ecoregions and fish communities in Wisconsin and found it to be only fair. In Ohio, Arkansas and Oregon, a DCA revealed that fish distributions corresponded with ecoregions somewhat better than they did with river basins, and much better than they did with physiographic regions (Hughes et al. 1990). Therefore, Oregon and Midwestern streams seem to be explained better by an ecoregion classification (mostly Omernik's classification) than any other classification, while eastern streams in the Mid-Atlantic region are not as well suited to the ecoregional approach. As a caveat, very few studies have incorporated the Bailey ecoregion classification in their comparisons (this study and Rabeni and Doisy

2000). It should be noted that this study is the first to explore fish patterns relative to ecoregions in a large contiguous multiple-state area in the Midwest.

Impacts of scale and the efficacy of subregionalization

The classification strength analysis at the coarser scale (analogous to Omernik level II ecoregions and Bailey provinces) was incorporated into the study to compare the ecological utility of the different levels of the nested hierarchical classifications for streams (i.e., the efficacy of subregionalization). The results may elucidate certain environmental criteria that may be more influential to stream communities and ecosystems at one scale but not another. The rankings of the classifications came out differently based on the scale that was assessed (see Table 5), but the rankings at the coarser scale did not seem to be as greatly affected as the finer scale rankings by the index that was applied. Both indices applied here revealed that the Bailey, Omernik and HUC classifications performed much more poorly relative to the other geographic classifications (the Maxwell and geographic cluster classifications) at the coarser scale than they did at the finer scale. There was a decrease in the average % maximum CS based on the Sørensen analysis among the regional classifications when moving from finer to coarser subdivisions (Table 6). The exceptions to this finding, the Maxwell classification and the geographic clusters, increased their own % maximum CS values when this coarser scale was used.

In contrast to the Sørensen results, the average % maximum CS based on Bray-Curtis similarities went up by at least 10% when looking at a coarser scale. Again, the Maxwell classification and the Geographic distance clusters increased their % maximum CS with the scale change (a substantial increase of 19% and 26% respectively). The exception to this trend was seen in the Bailey Provinces, which decreased 8% when moving to the coarser scale.

From this two-scale comparison, it seems that the Maxwell and Geographic distance clusters are more applicable to stream systems at the coarser scale (i.e., Maxwell subregions) than the finer scale (i.e., Maxwell river basins). The performance of the Geographic distance clusters may point to an even greater tendency toward spatial autocorrelation in stream fish communities in this part of the Midwest at the coarser scale. However, the Maxwell classification showed this trend toward better correspondence with fish communities at the coarser scale as well, which may have been caused by the inclusion of large biogeographic patterns in aquatic biota as one of the criteria for defining the Maxwell subregions. Finally, the larger sample size (N=219 streams) used for the coarser scale geographic cluster analysis may have contributed to a better performance at the coarse scale than the fine scale (N=165 streams) for the geographic clusters.

Since the Maxwell classification out-performed the Bailey and Omernik classifications at the coarser scale, it may be suggested that those criteria unique to the Maxwell classification (zoogeographic patterns and heavy use of watershed boundaries) are more informative as to patterns in stream ecosystems and communities at the coarser scale than at a finer scale where the Maxwell classification performed poorly compared to the other regional classifications.

Patterns of species abundance vs presence/absence at different scales

Other interesting patterns were revealed by the two-scale analysis. The average % maximum classification strength (CS) decreased for the Sørensen analysis when moving to the coarser scale, but increased for the Bray-Curtis analysis by a large percentage (although the % of the maximum CS values were mostly higher using the Sørensen index compared to the Bray-Curtis index at both scales). This indicates that regional classifications are more useful in circumscribing patterns in fish relative abundance at a coarser scale than at a finer scale, but that they circumscribe patterns in species presence/absence better at the finer than the coarser scale. Why were differences in species composition more apparent when subdividing regions at the finer scale? Why were differences in abundance more apparent at the coarser scale? Perhaps this indicates the patchy nature of some species assemblages that are better circumscribed by finer scale regional divisions (i.e., a small ecoregion), but that occur in such low abundance that they have little influence on the Bray-Curtis proportional abundance metric at that finer scale. These patterns also may indicate that the four-state study area contains species that are distributed widely throughout the region, but that patterns in the abundance of these species vary over larger areas. Ecological factors are perhaps controlling success but not dispersal ability of these species at that coarser scale. This is not surprising, since large portions of the study area have no distinct topographic variation among watersheds.

It is interesting that the Bailey classification performed most poorly at a coarser scale when all the other classifications performed better at that coarser scale based on the Bray Curtis analysis. The Bailey classification at the coarse scale (Bailey provinces) differs from the others in that Bailey puts more emphasis on climate in delineating his regions. Perhaps this indicates that climatic features at the coarser scale are not as important as other ecological factors in controlling the success (if not the dispersal) of fish species in the Midwest. Bailey also leaves out landform and geology as defining criteria at this scale while other classifications include these at the coarser scale. In general, Bailey uses fewer criteria at this coarser scale than other classifications, which could be hindering the classification's ability to account for patterns in fish abundance.

Published studies are not consistent as to what scale elucidates patterns in stream ecosystems better. Feminella (2000) conducted a multiple scale comparison of stream classifications in Tennessee, Georgia, and Alabama using macroinvertebrates and found that the four ecoregions (Omernik level III – 1995) he assessed performed equally well compared to the seven finer scale catchments he employed. However, Feminella's sample size was quite low, and therefore the finer level of resolution (the catchment) held a very small number of sites per region (four to six sites), which could have skewed the analysis. Using invertebrates in Oregon, Whittier et al. (1988) also found that subregionalization did not improve their ability to classify streams. As in Feminella's study, Marchant et al. (2000) subdivided their study area (Victoria, Australia) into smaller catchments and larger ecoregions. However, they found that the finer scale catchment was far superior at partitioning variation among invertebrate stream communities. In addition, subdividing Bailey's (1995) ecoregions (ecological sections) into smaller subsections yielded a better correspondence with stream benthic invertebrates in Missouri (Rabeni and Doisy 2000).

The average CS for the non-regional taxonomic fish clusters decreased when moving to a coarser scale using both similarity indices. Therefore, types of fish communities were better described at the finer scale. Thus, that finer scale may be a better scale at which to concentrate stream assessment and research efforts if stream fish communities and other biota are the focus of attention, or are being used as representatives of the stream system as a whole.

Comparison of specific regions

This part of the discussion will focus on the results from the finer-scale classifications, because that scale is generally applied more in stream research and monitoring efforts by management agencies (i.e., R-EMAP- the Regional Environmental Monitoring and Assessment Program - run by the USEPA). Based on the similarity dendrograms (Fig.s 7 and 8), certain finer scale regions in the study area have a distinctly higher individual CS. As mentioned above, the geographic areas with the longest branches (highest individual CS) fell within the south central part of the study area (the Flint Hills area in eastern Kansas) and the northeastern part of the study area (the glaciated areas of central and northeastern Iowa) based on both the Bray-Curtis and the Sørensen analyses (see starred regions on Fig.s 1 through 5). However, an area that is just east of the center of the study area (roughly coinciding with the Missouri-Nishnabotna basin) performed best based on the HUC and the Maxwell dendrograms constructed from Sørensen similarities (see Fig.s 3 and 4). The groups that usually performed worst (had the lowest individual CS values) across all classifications were located in the western high plains of Nebraska and Kansas and the Nebraska Sand Hills area.

A high individual classification strength (CS) could either mean that the region has a more consistent community structure across its area (its communities are more homogeneous among streams), and/or that the species within the communities are unique and do not generally occur in other regions. The Flint Hills area may have had a higher individual CS because this area has had less broad scale disturbance compared to other regions, and therefore its rarer species have not been regionally extirpated. Also, it contains a unique geology (shale outcrops and cherty limestone), shallow soil, and unique land use (limited cropland) compared to surrounding regions. The superior performance of the Flint Hills was also noted in an analysis done by David Peck of the USEPA (Pers. Comm).

Northeastern parts of Iowa (containing the Driftless Area) may have shown a higher individual CS because of the unique glacial influence prevalent in that area. Glacial refugia influence vicariant speciation, resulting in unique species assemblages. In addition, glacial action can form streams with distinctly different substrates. The Driftless Area also showed a high individual CS in a study of Wisconsin ecoregions done by Weigel (2003).

Conservation implications

An obvious next question would be whether these areas with high individual CS are of high conservation value. Griffith (2003) identified the Ozark plateau, the Nebraska Sandhills, and portions of south-central Kansas in the Central Great Plains and Flint Hills as areas of fish conservation concern using index of biotic integrity (IBI) scores, species richness, and endemic, threatened, or endangered species occurrences from Kansas, Missouri, and Nebraska Regional Environmental Monitoring and Assessment Program (REMAP) data from the USEPA. In this study, the Nebraska Sand Hills area showed one of the lowest individual CS values, which is the opposite of what might be expected from an area of high fish conservation concern. This poor performance could be due to the sandy homogeneous substrate that is prevalent in most Nebraska Sandhills streams. Perhaps a look at the species composition of these areas could be helpful to tease apart what is really happening in the streams. If some areas house more rare species and a greater biodiversity than other regions, they are of greater value (although that may not be apparent in the CS outcome). In this way, the CS evaluation of ecoregions may be useful for showing general trends in communities related to broad scale environmental factors, but not for highlighting threatened or imperiled species assemblages. Again, a closer examination of the species assemblages will help.

The information detailing regionally unique and regionally distinctive widespread species contained in Tables 7 and 8 helps to reveal differences among the ecoregions by elucidating the actual species present in them, and will provide further information regarding the utility of the Omernik ecoregional design for streams, which is one of the regional frameworks that is most widely used by the USEPA and state natural resource agencies for structuring stream monitoring and management.

Some overall patterns for each ecoregion are revealed in Tables 7 and 8. The Western High Plains and the Nebraska Sandhills have the fewest widespread species (2 species each), while the Flint Hills and the Interior River Valleys and Hills have the most (14 and 11 species respectively). An examination of the distinctive widespread species and the unique species will further reveal how well ecoregional design corresponds with variation in stream communities.

The ratio of Distinctive Widespread species (DWS) to the total number of species (richness) in a region can reveal both the **spatial evenness** of an ecoregion species assemblage and also its distinctiveness. A high ratio would indicate that there was a distinct fish community in the region as a whole that was evenly distributed throughout the streams – a relatively biologically diverse assemblage that is spread out in a homogeneous way. The Flint Hills had the highest ratio of DWS/Richness (see Table 9), which corroborates its superior individual classification strength as depicted in the similarity dendrogram for Omernik Ecoregions (Fig. 7).

The ratio of widspread species to richness also seems informative, because the three ecoregions with the highest WS/Richness ratio (the Flint Hills, Central Irregular Plains and the Interior River Valleys and Hills - see Table 9) outperformed all other regions according to the similarity dendrogram (see Fig. 7). However, this ratio only provides information about spatial evenness of an assemblage – not its compositional distinctiveness, indicating that the CS analysis is weighted toward the homogeneity among communities spread across an ecoregion rather than the distinctive or rare species present in the region.

The Flint Hills contained relatively few unique species (three) compared to its large number of distinctive widespread species (seven). This low number of unique species did not seem to damage the Flint Hills' CS ranking. The ratio of the number of unique species to total richness (US/Richness – Table 9) can also be used to examine the validity of regional separations that have been made. The Ozark Highlands had the most unique species assemblage according to this ratio, followed by the Western Cornbelt Plains and the Driftless area. With the exception of the Driftless Area, these ecoregions did not perform in the top three based on the similarity dendrograms (Fig.s 7 and 8) for either the Bray-Curtis or the Sørensen analysis. They generally fell somewhere in the middle of the individual CS rankings.

Given the above trends, it can be concluded that a high individual classification strength (CS) is not as closely linked to the uniqueness of the components of an assemblage, but rather the presence of a relatively biodiverse, distinctive and well-dispersed regional assemblage that forms communities with similar composition throughout a regional unit - at least in this part of the Midwest. This is not to say that a high CS is not linked to the conservation value of a region. Most likely, the conservation value of an area will depend on whether the goal is to preserve the most species or to preserve an intact and distinct ecological unit. If the goal is to preserve that intact ecosystem, the CS analysis does provide useful information for conservation efforts. In the case of the Flint Hills, this high individual CS may indicate that the region's stream habitats are relatively homogeneous and there are not many physical barriers to fish dispersal historically in the area. However, a region with an assemblage that includes many unique and rare but somewhat restricted species such as the Western Cornbelt Plains, Ozark Highlands, and Central irregular Plains probably has more habitat heterogeneity among streams and would most likley benefit from finer scale regionalization (i.e., Omernik level IV regions) and subsequent CS analysis.

Unique contributions of this study

This study is unique in that it compares current stream classification approaches, which should account for natural environmental variation in their design, in an area of the US that has been focussed on very little in this regard (Kansas, Nebraska, Missouri and Iowa). The analysis here combined data from many different agencies across state lines at a coarser scale than most analyses done on streams. Usually, this type of analysis is done within one state or geopolitical boundary (i.e., Weigel 2003; Whittier et al. (1988); and Vansickle and Hughes 2000) because it is often funded by state agencies. This study also compares classifications that were not included in studies in the North American Benthological Society's special 2000 issue, including a more aquatic oriented classification (e.g., the Maxwell et al. 1995 classification) than was tested in those studies. In fact, no studies that compare the aquatic ecological units of Maxwell et al. (1995) to other stream classifications have been found in the literature. Finally, this study includes the Bailey ecoregions classification, which has only been compared to the Omernik approach for its applicability to streams by one other study - Rabeni and Doisey (2000).

Conclusions

Identifying patterns in natural variation in stream ecosystems provides an influential tool to promote management action by supplying a benchmark to work toward, and an assurance that the stream of concern is a degraded (not just a naturally different) system. It is therefore important to test the validity of the stream classifications that are being applied in this pursuit.

All of the regional stream classifications tested here performed better than a random reassignment of sites to groups, meaning that they had some value in classifying stream fish communities. However, the **raw** classification strength (CS) values were relatively weak (high of 20 % for the Sørensen analysis of the finer scale classifications).

The Geographic Distance Clusters performed consistently better than any of the other classifications in the study (with the exception of the taxonomic clusters) based on the classification strength analyses (see Table 5). The geographic clusters were the only classification system to show a superior correspondence with patterns in fish communities across both spatial scales assessed in this study (although not across both indices). This indicates that there is a high degree of spatial autocorrelation in the fish communities in this part of the Midwest.

The more aquatic Maxwell et al. classification performed the most poorly of all regional classifications at the finer scale based on the Sørensen analysis, and not as well as the other ecoregion classifications based on the Bray-Curtis analysis. This result may indicate that specifically aquatic criteria are not as useful as the suite of terrestrial and climate criteria assumed by the other classifications to shape regional patterns in stream ecosystems in the Midwest at this scale.

The non-regional *a priori* Strahler stream orders classified the streams most poorly. Therefore, longitudinal location of a stream in a stream network, stream size and discharge do not seem as important to landscape-scale fish community patterns within the area studied here compared to ecoregion location.

Based on the relative abundance data, the Omernik ecoregions outperformed all other classifications at the finer scale, but had only a slightly higher % of the maximum CS than the Bailey ecoregions. Because the Bailey and Omernik ecoregional frameworks were almost equally predictive of fish patterns in the study area, there does not seem to be an advantage to the increased emphasis placed on climate in the Bailey scheme nor land use in the Omernik scheme for predicting patterns in stream biota. Alternatively, this result could be interpreted to mean that contemporary human land use may be as important as climate in shaping stream communities.

A subanalysis done on northeastern Iowa indicated that the Omernik approach would likely benefit from a stronger consideration of glacial influences during further ecoregion delineation attempts in this and other glacially impacted areas if the purpose for an ecoregion delineation is to account for variation in stream ecosystems.

The Bailey classification performed most poorly at a coarser scale, while all the other classifications performed better at that coarser scale based on the Bray Curtis analysis. Because the Bailey classification at the coarse scale (Bailey provinces) puts more emphasis on climate in delineating regions, perhaps this indicates that climatic features at the coarser scale are not as important as other ecological factors in controlling the success (if not the dispersal) of fish species in the Midwest.

The results suggest that physical boundaries to species dispersal may be having an impact on stream biota that is nearly as important as the suite of strictly ecological factors that are represented in the ecoregions frameworks. Further work (Chapter Two) will test the ecoregion frameworks stratified by HUCs to see if this new hybrid classification will have stronger predictive powers for stream communities in this part of the Midwest.

This study also revealed that the application of the type of ecological regions studied here seemed to be more appropriate for U.S. streams in the Midwest and Oregon than for streams in the East - particularly in the Mid-Atlantic Highlands.

Based on the detailed evaluation of the species assemblages, the classification strength assessment of ecoregions may be useful for showing general trends in communities related to large scale environmental factors, or for highlighting large homogeneous intact ecosystems like the Flint Hills, but not for highlighting rare or threatened species assemblages. This is important information for those attempting to apply the ecoregions analyzed here in a conservation context.

Overall, the results indicate that the ecoregion classifications are useful – that they do include criteria that account for variation in fish community patterns - especially based on species presence/absence. However, they also indicate that there is still quite a lot of variation unaccounted for by the classifications tested here – particularly related to the realized niche of a species/assemblage as revealed by patterns in abundance. Obviously, there are aspects of the ecoregion delineation process that need to be altered to improve their applicability to streams. However, the weak performance of all the classifications leads to a question: “Has human-mediated extirpation and translocation of assemblages muddied the distinct differences in fish communities that may have been present historically among ecologically distinct regions?” This question is addressed in Chapter Three, which looks at biotic homogenization in this part of the Midwest.

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TABLES AND FIGURES FOR CHAPTER ONE

Classification Schemes		Area (mi^2)	Defining Criteria
Omernik Ecoregions	Level II	10,000s - 100,000s	landform, geology, land use/cover, climate, soils, potential natural vegetation (focus on land cover, but the criteria used varies somewhat based on its importance to the region)
	Level III	1,000s - 10,000s	
Bailey Ecoregions	Provinces	10,000s	climate, soils and potential natural vegetation (focus on geoclimatic setting)
	Sections	1,000s - 10,000s	climate, geology, landform, soils, potential natural vegetation, and some land use/cover (focus on geoclimatic setting and glacial influences)
Watersheds (HUCs)	2-digit	10,000s - 100,000s	topography (extraction from digital elevation models (DEM's))
	4-digit	1,000s	extraction at a finer scale
Maxwell et al. (Aquatic Ecological Units)	Subregions	10,000s	geology, landform, climate, biogeographic patterns for aquatic biota and watershed boundaries
	River Basins	1,000s-10,000s	
Non-spatial Random Clusters	Larger Clusters	N/A	random assignment of sites into a comparable number of groups to other classification schemes (10000 iterations)
	Smaller Clusters	N/A	
Neutral Geographic-distance Clusters	Larger Clusters	10,000s	geographic distance between sites
	Smaller Clusters	1,000s	
Hybrid Classification: Omernik Ecoregions/Watershed (HUC 2)	Level II / HUC	1,000s - 10,000s	ecoregion stratified by 2-digit HUC boundaries
Hybrid Classification: Bailey Ecoregions/Watershed (HUC 2)	Provinces / HUC	1,000s - 10,000s	ecoregion stratified by 2-digit HUC boundaries
Strahler Stream Order	N/A	N/A	stream order identified by monitoring agency
Fish Similarity Clusters (Maximum CS)	Larger Clusters	N/A	maximum fish community similarity based on the flexible beta cluster analysis
	Smaller Clusters	N/A	

Table 1. Characteristics of stream classifications and hierarchical levels of interest to this study

Site	Ecoreg.	KS096S	NE086S	NE094S	NE081S	NE096S	KS078S	KS097S	KS100S	NE077S	NE080S	KS081S	KS085S	KS089S
KS096S	WHP	1.000	0.000	0.444	0.235	0.286	0.375	0.462	0.471	0.471	0.267	0.231	0.171	0.065
NE086S	WHP	0.000	1.000	0.250	0.125	0.400	0.267	0.333	0.125	0.250	0.286	0.080	0.000	0.000
NE094S	WHP	0.444	0.250	1.000	0.286	0.333	0.308	0.400	0.143	0.429	0.333	0.087	0.000	0.000
NE081S	WHP	0.235	0.125	0.286	1.000	0.308	0.286	0.333	0.000	0.273	0.300	0.323	0.300	0.222
NE096S	WHP	0.286	0.400	0.333	0.308	1.000	0.400	0.273	0.308	0.462	0.500	0.286	0.182	0.150
KS078S	CGP	0.375	0.267	0.308	0.286	0.400	1.000	0.588	0.667	0.762	0.737	0.467	0.256	0.286
KS097S	CGP	0.462	0.333	0.400	0.333	0.273	0.588	1.000	0.444	0.444	0.500	0.296	0.167	0.125
KS100S	CGP	0.471	0.125	0.143	0.000	0.308	0.667	0.444	1.000	0.545	0.400	0.323	0.250	0.222
NE077S	CGP	0.471	0.250	0.429	0.273	0.462	0.762	0.444	0.545	1.000	0.600	0.516	0.300	0.333
NE080S	CGP	0.267	0.286	0.333	0.300	0.500	0.737	0.500	0.400	0.600	1.000	0.414	0.211	0.235
KS081S	FH	0.231	0.080	0.087	0.323	0.286	0.467	0.296	0.323	0.516	0.414	1.000	0.490	0.533
KS085S	FH	0.171	0.000	0.000	0.300	0.182	0.256	0.167	0.250	0.300	0.211	0.490	1.000	0.741
KS089S	FH	0.065	0.000	0.000	0.222	0.150	0.286	0.125	0.222	0.333	0.235	0.533	0.741	1.000

Table 2. Partial Sørensen similarity matrix (Omernik Level III Ecoregions). WHP=western high plains; CGP=central great plains; FH=flint hills

			Sorensen Similarities (Presence/Absence)					Bray-Curtis Similarities (Relative Abundance)				
Group Name	No. of Groups	No. of Streams	Overall mean similarity within groups (W)	Mean similarity among groups (B)	Class. Strength (CS)%	B/W	% of maximum attainable CS	Overall mean similarity within groups (W)	Mean similarity among groups (B)	Class. Strength (CS)%	B/W	% of maximum attainable CS
Geographic Distance Clusters	8	165	0.50	0.30	20	0.60	79	0.23	0.11	11	0.51	43
Bailey Sections	12	223	0.49	0.30	19	0.62	75	0.22	0.12	11	0.52	55
Omernik Level III	9	210	0.46	0.29	18	0.62	75	0.21	0.11	10	0.51	57
4 digit HUCs	15	196	0.51	0.32	18	0.64	73	0.23	0.13	10	0.56	48
Maxwell River Basins	11	223	0.48	0.32	16	0.66	69	0.21	0.12	9	0.58	50
Strahler Order	5	115	0.36	0.29	7	0.81	30	0.15	0.11	4	0.74	27

Table 3. Mean similarity values and classification strengths for smaller stream classification subdivisions. The permutation tests for all a priori frameworks based on random site reassignments yielded a $p<0.000001$, indicating that the hypothesis of "no classification structure" was rejected. The % of maximum attainable CS is the CS of the framework as a percentage of the maximum possible CS value (based on the taxonomic fish clusters' CS values, which are listed in the Appendix). The B/W ratios also indicate the strength of a classification scheme; a larger value close to 1 indicates a classification with no inherent value in accounting for stream variability (possible values are from 0 to 1).

			Sorensen Similarities (Presence/Absence)					**Bray-Curtis Similarities (Relative Abundance)**				
Large Group Name	No. of Groups	No. of Streams	Overall mean similarity within groups (W_i)	Mean similarity among groups (B)	Class. Strength (CS)%	B/W	% of maximum attainable CS	Overall mean similarity within groups (W_i)	Mean similarity among groups (B)	Class. Strength (CS)%	B/W	% of maximum attainable CS
Maxwell Subregions	4	231	0.43	0.28	15	0.66	83	0.18	0.11	8	0.58	69
Geographic Distance Clusters	4	219	0.42	0.29	14	0.68	82	0.18	0.11	8	0.58	69
Omernik Level II	5	228	0.40	0.27	13	0.67	70	0.17	0.10	7	0.58	60
2 digit HUCs	3	231	0.39	0.29	11	0.73	55	0.16	0.11	6	0.66	61
Bailey Provinces	4	231	0.38	0.27	11	0.71	63	0.16	0.11	5	0.67	47
Strahler Order	5	115	0.36	0.29	7	0.81	30	0.15	0.11	4	0.74	27

Table 4. Mean similarity values and classification strengths for large stream classification subdivisions. The permutation tests for all a priori frameworks based on random site reassignments yielded a $p<0.000001$, indicating that the hypothesis of "no classification structure" was rejected. The % of maximum attainable CS is the CS of the framework as a percentage of the maximum possible CS value (based on the taxonomic fish clusters' CS values, which are listed in the Appendix). The B/W ratios also indicate the strength of a classification scheme; a larger value close to 1 indicates a classification with no inherent value in accounting for stream variability (possible values are from 0 to 1).

	Sorensen (Presence/Absence)	Bray-Curtis (Relative Abundance)
Coarser scale subdivisions	M~G>O>B>H>>S	M=G>H~O>>B>>S
Finer scale subdivisions	G>B=O~H>M>>S	O~B>M~H>G>>S

Table 5. Rankings of the % maximum CS values for the classifications tested here. O = Omernik, B = Bailey, M = Maxwell et al., G = geographic distance clusters, S = Strahler stream order, H = hydrologic unit codes (HUCs).

Large Group Name	% of maximum attainable CS (Sor)	% of maximum attainable CS (B-C)	Small Group Name	% of maximum attainable CS (Sor)	% of maximum attainable CS (B-C)
Maxwell Subregions	83	69	Maxwell River Basins	69	50
Geographic Distance Clusters	82	69	Geographic Distance Clusters	79	43
Omernik Level II	70	60	Omernik Level III	75	57
2 digit HUCs	55	61	4 digit HUCs	73	48
Bailey Provinces	63	47	Bailey Sections	75	55
Means	70.6	61.4	Means	74.3	50.6
std dev	11.97	9.02	std dev	2.27	6.46
confidence int	10.49	7.91	confidence int	1.99	5.66

Table 6. A comparison of the % of the maximum attainable CS for five regional stream classifications at different scales (small vs. large subdivisions)

Western High Plains	**Neb. Sand Hills**	**Central Great Plains**	**Flint Hills**	**Western Corn Belt Plains**	**Central Irregular Plains**	**Ozark Highlands**	**Inter. River Valleys**	**Driftless Area**
Widespread spp.	**Widespread spp.**	**Widespread spp.**	**Widespread spp.**	**Widespread spp.**	**Widespread spp.**	**Widespread spp.**	**Widespread spp.**	**Widespread spp.**
Semotilus atromaculatus	*Pimephales promelas*	*Pimephales promelas*	*Campostoma anomalum*	*Semotilus atromaculatus*	*Campostoma anomalum*	*Campostoma anomalum*	*Lepomis cyanellus*	*Catostomus commersoni*
Pimephales promelas	*Catostomus commersoni*	*Cyprinella lutrensis*	*Cyprinella lutrensis*	*Notropis Stramineus*	*Lepomis cyanellus*	*Lepomis cyanellus*	***Ameiurus Natalis***	***Etheostoma flabellare***
		Notropis stramineus	*Etheostoma spectabile*	**Notropis dorsalis**	*Micropterus salmoides*	*Lepomis macrochirus*	*Semotilus atromaculatus*	***Rhinichthys cataractae***
		Lepomis cyanellus	*Pimephales notatus*	*Lepomis cyanellus*	*Pimephales notatus*	Noturus exilis	*Pimephales notatus*	*Semotilus atromaculatus*
			Ictalurus punctatus	*Pimephales promelas*	*Cyprinella lutrensis*		*Campostoma anomalum*	
			Lepomis cyanellus	*Catostomus commersoni*	*Lepomis macrochirus*		*Lepomis macrochirus*	
			Phenacobius mirabiles		*Etheostoma spectabile*		*Lythrurus umbratilis*	
			Lepomis megalotis				*Catostomus commersoni*	
			Percina caprodes				*Cyprinella lutrensis*	
			Lepomis Humilis				*Micropterus salmoides*	
			Micropterus salmoides				*Etheostoma spectabile*	
			Lythrurus umbratilis					
			Noturus flavus					
			Pylodictis olivaris					

Table 7. Widespread fish species of Omernik level III ecoregions within Kansas, Missouri, Iowa and Nebraska. Widespread species are present in at least 70% of the sampled streams in a region (from largest % to smallest % - top to bottom), and are representative of the typical community of species that might be found within a stream in the region of interest. Species are listed in order of most widespread to least widespread. Distinctive widespread species are in bold. Table C in the Appendix contains the rank stream occupancy data used to make this tabl

Western High Plains	**Neb. Sand Hills**	**Central Great Plains**	**Flint HIlls**	**Western Corn Belt Plains**	**Central Irregular Plains**	**Ozark Highlands**	**Inter. River Valleys**	**Driftless Area**
Unique spp.	**Unique spp.**	**Unique spp.**	**Unique spp.**	**Unique spp.**	**Unique spp.**	**Unique spp.**	**Unique spp.**	**Unique spp.**
Notropis bairdi	***Margariscus margarita***	***Macrhybopsis aestivalis***	***Noturus miurus***	***Cyprinella spiloptera***	***Percina shumardi***	***Cottus hypselurus***	***Notropis heterolepis***	***Cottus cognatus***
Catostomus catostomus	***Phoxinus neogaeus***	***Morone americana***	***Pimephales tennellus***	***Rhinichthys atratulus***	***Percopsis omiscomaycus***	***Cyprinella galactura***	*Notropis boops (rsr)*	***Lota lota***
Hybognathus hankinsoni (rsr)	*Esox americanus(rsr)*	*Etheostoma cragini (rsr)*	***Notropis Volucellus***	***Hybognathus nuchalis***	***Cycleptus elongatus***	***Etheostoma punctulatum***		***Notropis blennius***
	Noturus gyrinus (rsr)	*Fundulus zebrinus (rsr)*	*Minytrema melanops (rsr)*	***Lampetra appendix***	***Etheostoma chlorosomum***	***Etheostoma stigmaeum***		***Notropis Wickliffi***
	Phoxinus eos (rsr)	*Hiodon alosoides (rsr)*	*Luxilus cardinalis (rsr)*	***Macrhybopsis storeriana***	***Etheostoma whipplei***	***Etheostoma tetrazonum***		***Salvelinus fontinalis***
	Lepomis gibbosus (rsr)	*Hybopsis dorsalis (rsr)*	*Noturus nocturnus (rsr)*	***Perca flavescens***	***Lepomis microlophus***	***Fundulus catenatus***		*Cottus bairdi (rsr)*
		Hybognathus placitus (rsr)	*Notropis buchanani (rsr)*	***Stizostedion canadense***	***Menidia beryllina***	***Luxilus pilsbryi***		*Etheostoma asprigene (rsr)*
		Lepisosteus platostomus (rsr)	*Percina copelandi (rsr)*	***Umbra limi***		***Luxilus zonatus***		
		Phoxinus erythrogaster (rsr)	*Ictiobus niger (rsr)*	***Amia calva***	*Ictiobus niger (rsr)*	***Notropis greenei***		
				Carassius auratus	*Etheostoma blennioides (rsr)*	***Notropis telescopus***		
				Carpiodes velifer	*Lepisosteus platostomus (rsr)*	***Noturus albater***		
				Esox americanus (rsr)	*Lepomis gulosus (rsr)*	***Nocomis asper***		
				Esox lucius (rsr)	*Minytrema melanops (rsr)*	*Etheostoma blennioides (rsr)*		
				Etheostoma asprigene (rsr)	*Notropis buchanani (rsr)*	*Luxilus chrysocephalus (rsr)*		
				Etheostoma caeruleum (rsr)	*Noturus nocturnus (rsr)*	*Lepomis gulosus (rsr)*		
				Etheostoma exile (rsr)		*Luxilus cardinalis (rsr)*		
				Hiodon alosoides (rsr)		*Cottus carolinae (rsr)*		
				Hybopsis dorsalis (rsr				

Table 8. See caption on next page

				Hybognathus placitus (rsr)				
				Lepomis gibbosus (rsr)				
				Moxostoma anisurum (rsr)				
				Noturus gyrinus (rsr)				
				Platygobio gracilis (rsr)				
				Stizostedion vitreum (rsr)				

Table 8. Unique fish species of Omernik level III ecoregions within Kansas, Missouri, Iowa and Nebraska. A fish species is designated as unique if it does not occur in other subregions. The label rsr (rare and somewhat restricted) is appended to the species name if a species occurs in one or two regions outside the region of interest but only in a few streams in those regions. Unique species are in bold. Table C in the Appendix contains the rank stream occupancy data used to make this table.

Overall statistics											
Richness	Avg. richness/ stream reach	Richness min.	Richness max.	Avg. density/ stream reach	Avg. Shannon-Weiner index	S-W Min.	S-W Max.	Avg. Evenness			
142	16.5	2	36	796	1.77	0.27	2.62	0.66			
Statistics by region											
Region	Richness	Avg. richness/ stream	Avg. Density/ stream	Avg. Shannon-Weiner index	Avg. evenness	# of WS	# of DWS	# of US	DWS/ Richness	US/ Richness	WS/ Richness
WHP	30	6.4	489	1.149	0.693	2	0	2	0.00	0.07	0.07
NSH	36	9.4	451	1.249	0.566	2	0	2	0.00	0.06	0.06
DA	46	14.3	742	1.608	0.621	4	2	5	0.04	0.11	0.09
IRVH	47	19.8	1069	1.95	0.668	11	1	1	0.02	0.02	0.23
CGP	51	11.8	962	1.303	0.553	4	0	2	0.00	0.04	0.08
FH	56	25.2	2109	1.92	0.594	14	7	3	0.13	0.05	0.25
OH	62	17.6	578	1.699	0.611	4	1	12	0.02	0.19	0.06
CIP	68	21	755	2.113	0.708	7	0	7	0.00	0.10	0.10
WCBP	83	18.3	735	2.002	0.712	6	1	11	0.01	0.13	0.07

Table 9. Reference stream fish community statistics over the 4-state study area. WS is widespread species. DWS is distinctive widespread species. US is unique species.

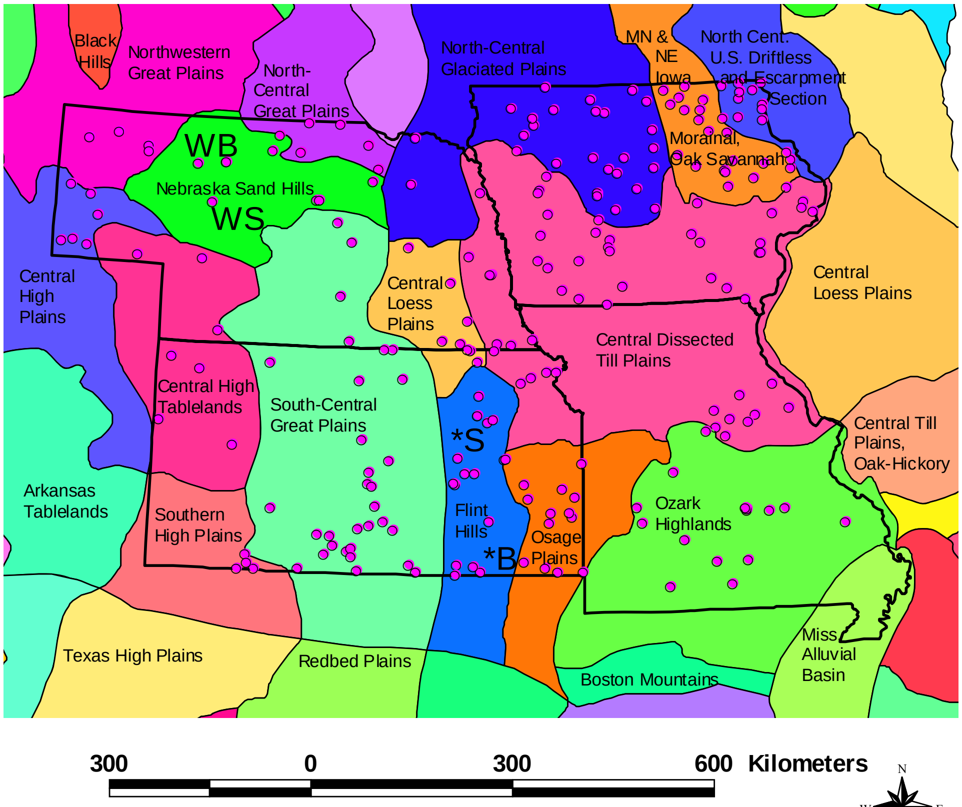
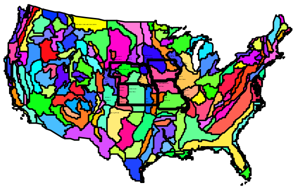


Figure 1. Bailey sections within the 4-state study area with reference sites



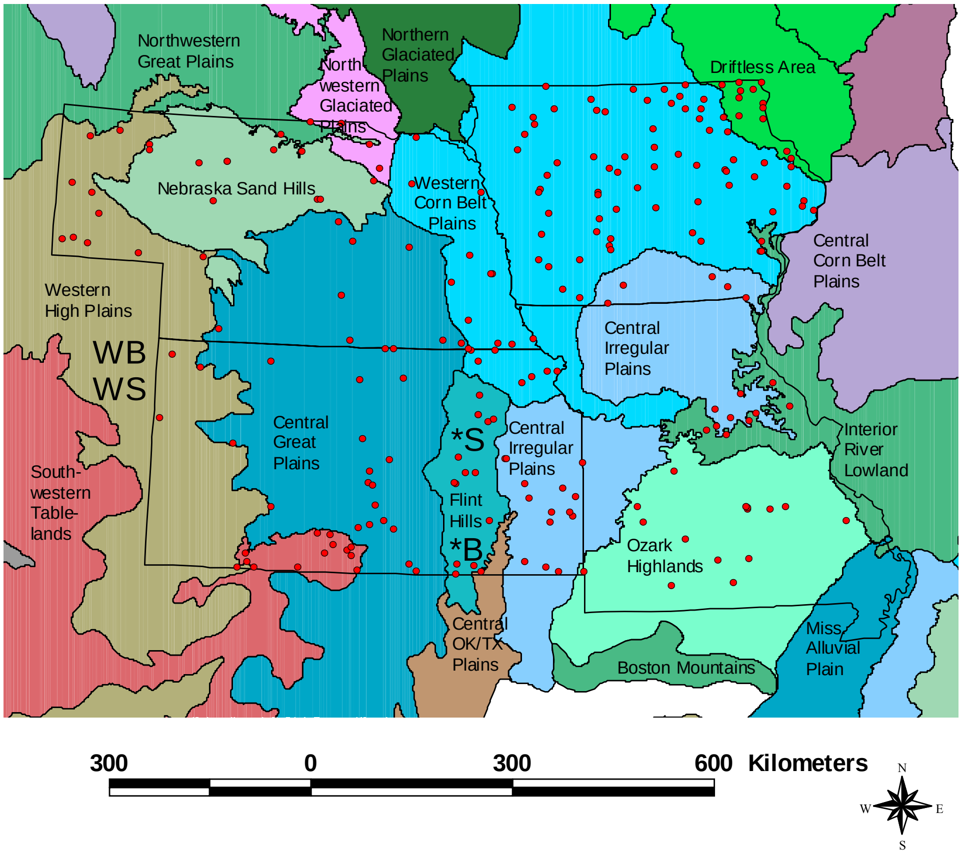


Figure 2. Omernik level III ecoregions within the 4-state study area with reference sites

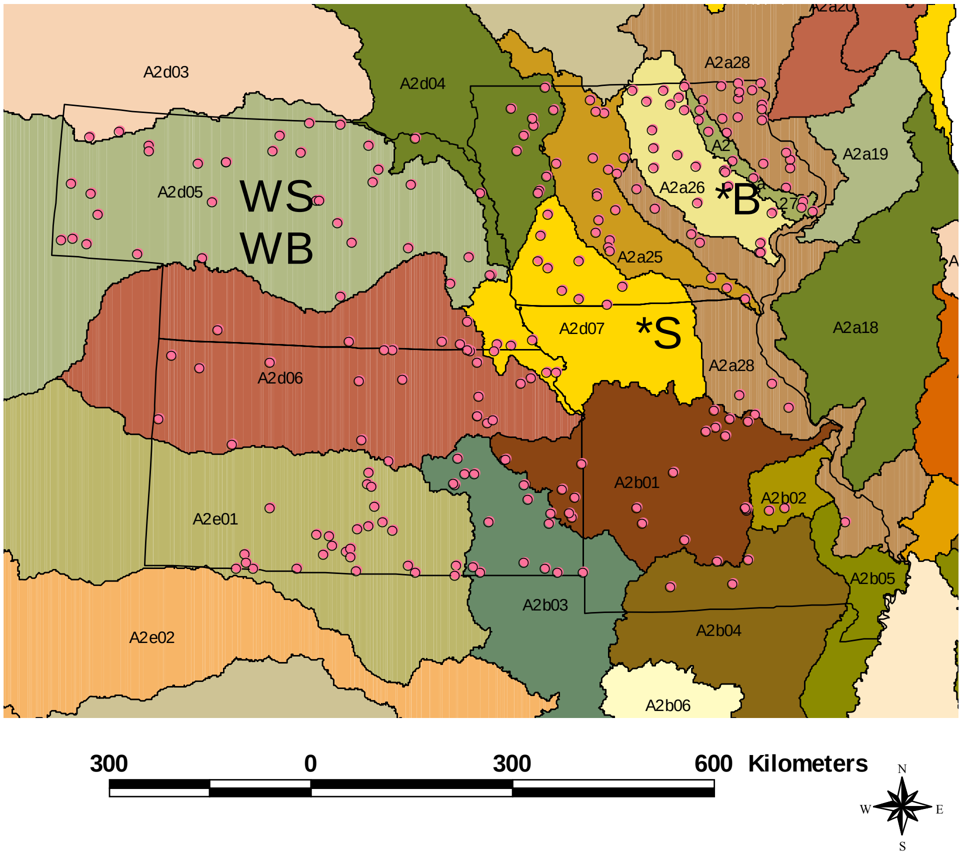


Figure 3. Maxwell et al. river basins within the 4-state study area with reference sites

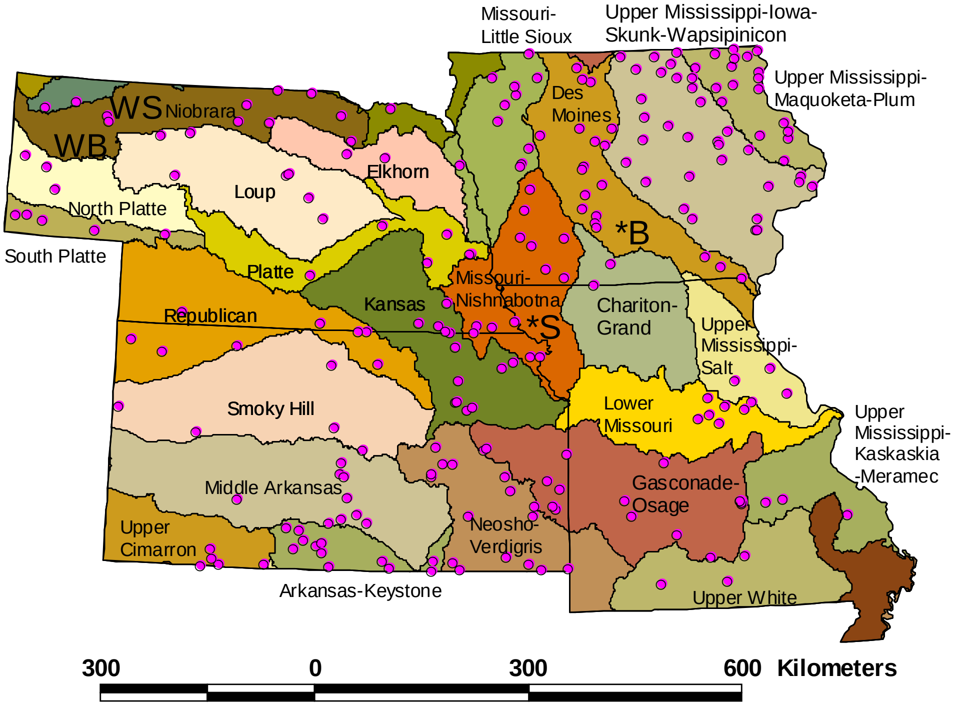


**Figure 4. 4-digit HUCs within the
4-state study area with reference sites**

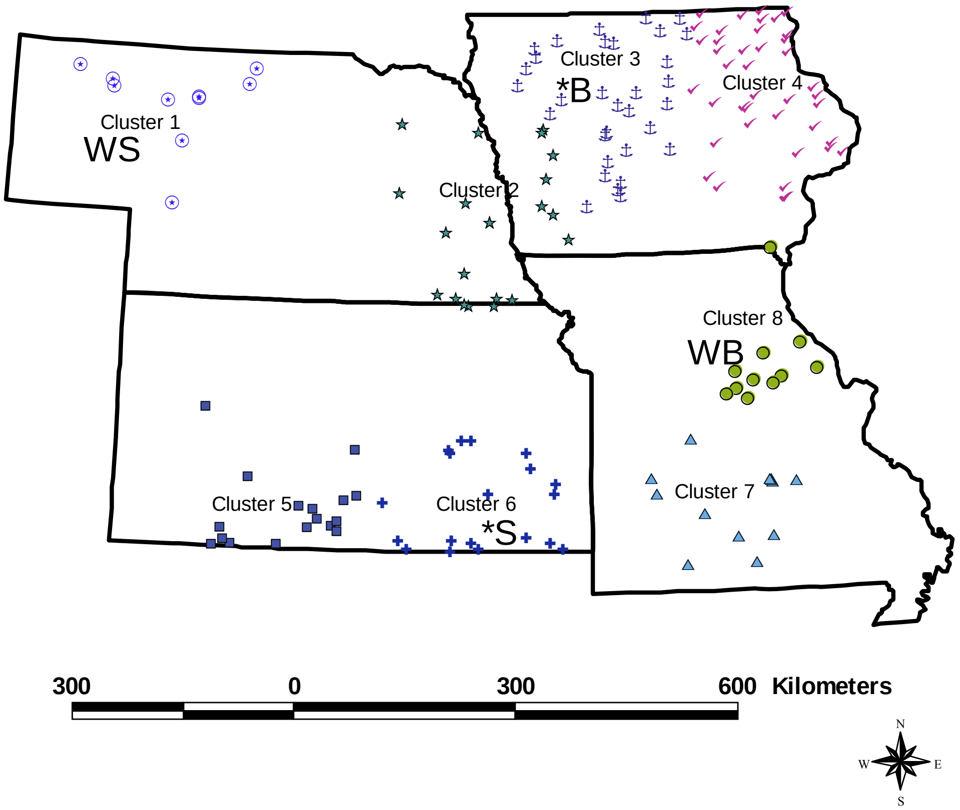


Figure 5. Small geographic distance clusters within the 4-state study area with reference sites

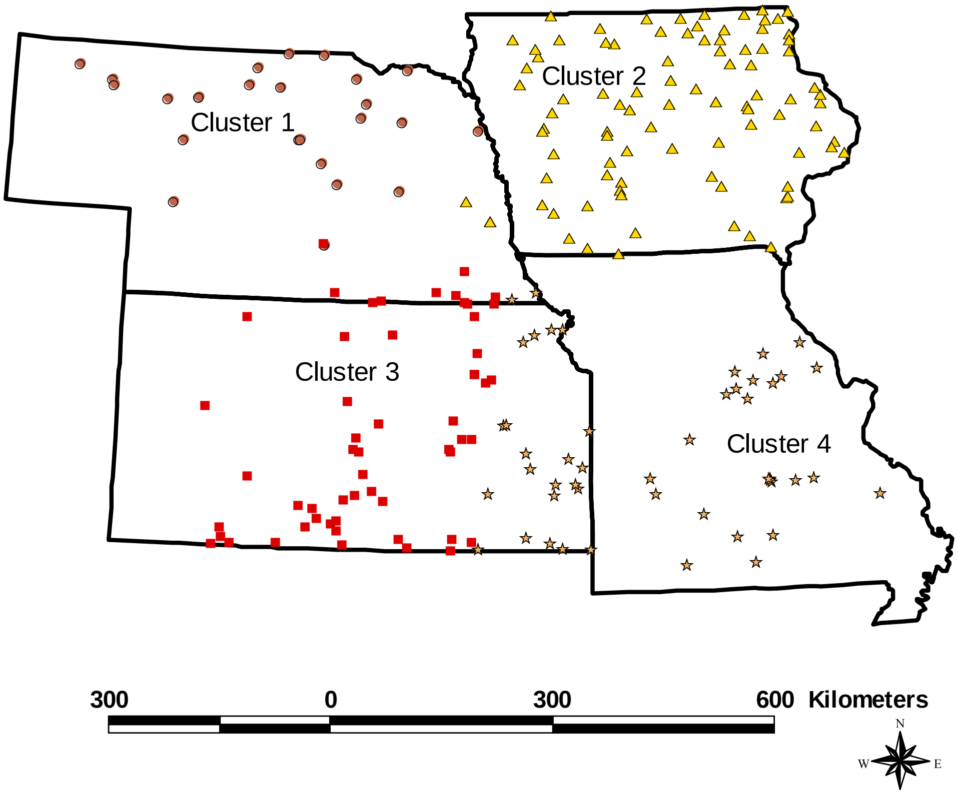


Figure 6. Large geographic distance clusters within the 4-state study area with reference sites

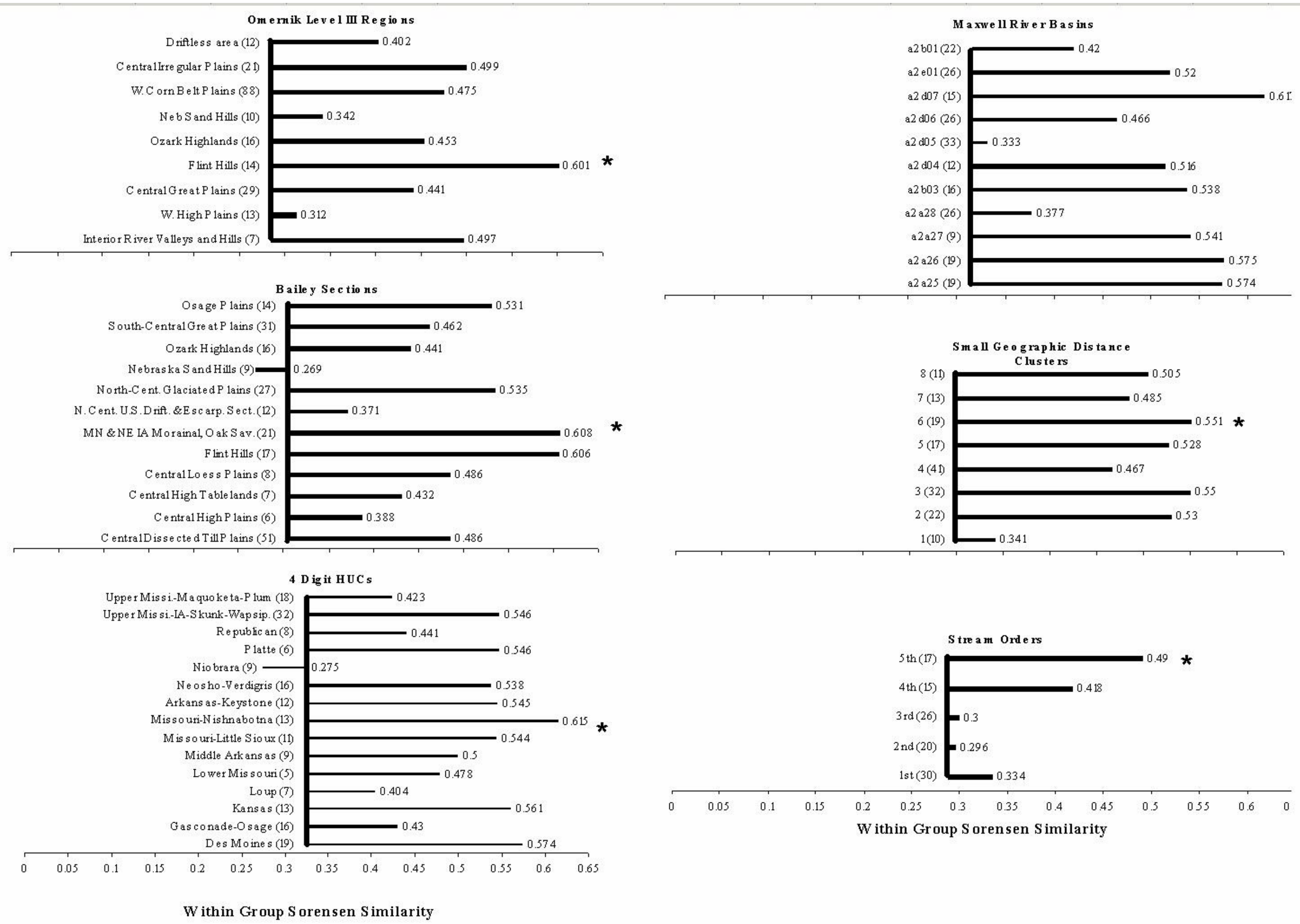

Omernik Level III Regions
Driftless area (12)
0.402
Central Irregular Plains (21)
0.499
W. Corn Belt Plains (88)
0.475
Neb Sand Hills (10)
0.342
Ozark Highlands (16)
0.453
Flint Hills (14)
0.601
*
Central Great Plains (29)
0.441
W. High Plains (13)
0.312
Interior River Valleys and Hills (7)
0.497
Bailey Sections
Osage Plains (14)
0.531
South-Central Great Plains (31)
0.462
Ozark Highlands (16)
0.441
Nebraska Sand Hills (9)
0.269
North-Cent. Glaciated Plains (27)
0.535
N. Cent. U.S. Drift. & Escarp. Sect. (12)
0.371
MN & NE IA Morainal, Oak Sav. (21)
0.608
*
Flint Hills (17)
0.606
Central Loess Plains (8)
0.486
Central High Tablelands (7)
0.432
Central High Plains (6)
0.388
Central Dissected Till Plains (51)
0.486
4 Digit HUCs
Upper Missi.-Maquoketa-Plum (18)
0.423
Upper Missi.-IA-Skunk-Wapsip. (32)
0.546
Republican (8)
0.441
Platte (6)
0.546
Niobrara (9)
0.275
Neosho-Verdigris (16)
0.538
Arkansas-Keystone (12)
0.545
Missouri-Nishnabotna (13)
0.615
*
Missouri-Little Sioux (11)
0.544
Middle Arkansas (9)
0.5
Lower Missouri (5)
0.478
Loup (7)
0.404
Kansas (13)
0.561
Gasconade-Osage (16)
0.43
Des Moines (19)
0.574
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0.55
0.6
0.65
Within Group Sorensen Similarity
Maxwell River Basins
a2b01 (22)
0.42
a2e01 (26)
0.52
a2d07 (15)
0.61
a2d06 (26)
0.466
a2d05 (33)
0.333
a2d04 (12)
0.516
a2b03 (16)
0.538
a2a28 (26)
0.377
a2a27 (9)
0.541
a2a26 (19)
0.575
a2a25 (19)
0.574
Small Geographic Distance Clusters
8 (11)
0.505
7 (13)
0.485
6 (19)
0.551
*
5 (17)
0.528
4 (41)
0.467
3 (32)
0.55
2 (22)
0.53
1 (10)
0.341
Stream Orders
5th (17)
0.49
*
4th (15)
0.418
3rd (26)
0.3
2nd (20)
0.296
1st (30)
0.334
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0.55
0.6
0
Within Group Sorensen Similarity

Figure 7. Similarity Dendrograms showing within-group Sorensen similarities (W_i) for 6 classifications. The base of the dendrogram is located at the mean among-group similarity value (B) for the classification. The value shown at the end of the branches is the mean within-group similarity for the designated group or region (W_i). The longest branch of the dendrogram indicates the subregion or group with the most unique fish community, and the length of each branch is equal to $W_i – B$. This value represents a group's individual Classification Strength (CS). According to the dendrograms, the south central region of the study area (e.g., the Flint Hills) and northeastern Iowa generally have the highest within-region similarity among stream fish communities and the most unique fish assemblages.

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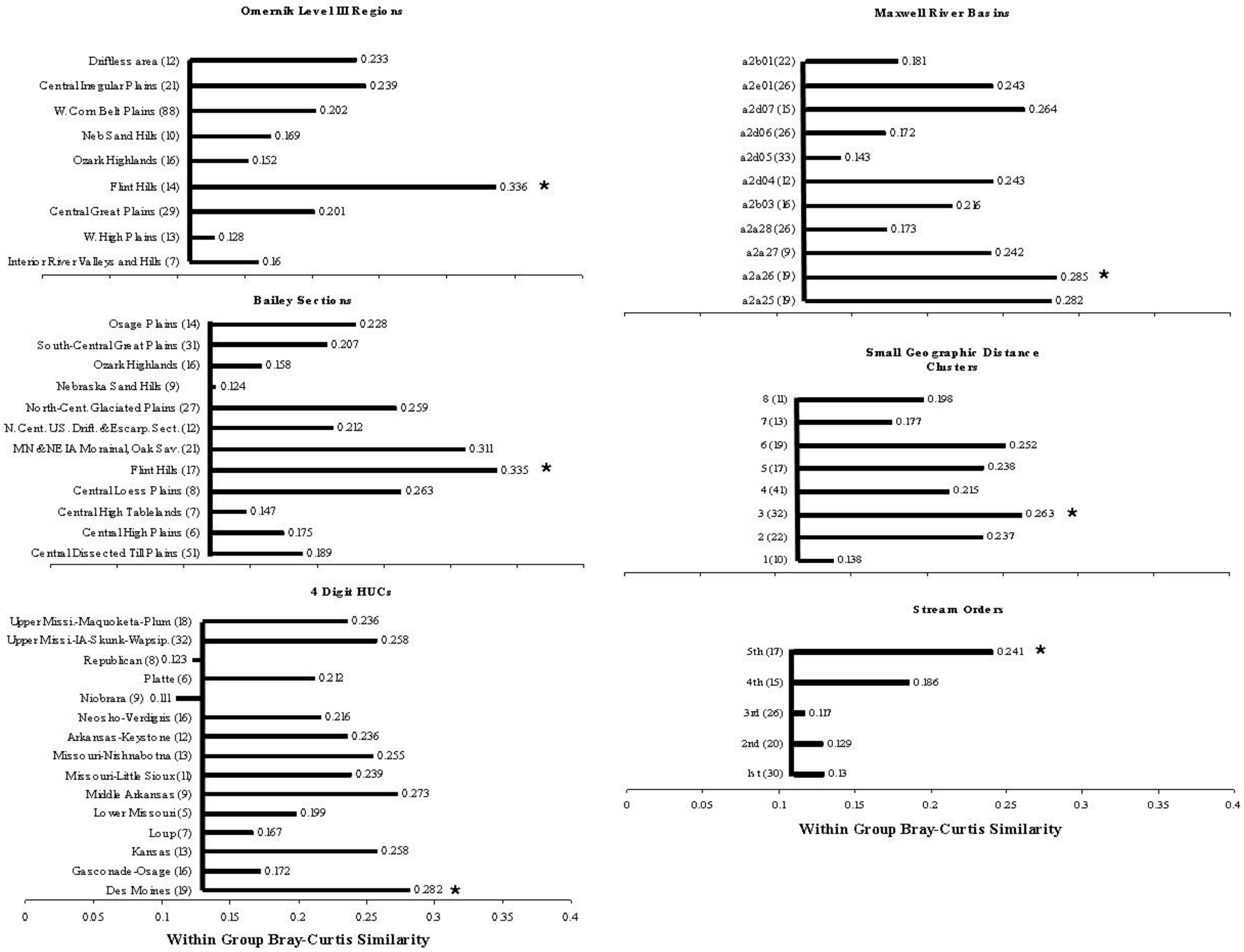
Omernik Level III Regions
Driftless area (12) 0.233
Central Irregular Plains (21) 0.239
W. Corn Belt Plains (88) 0.202
Neb Sand Hills (10) 0.169
Ozark Highlands (16) 0.152
Flint Hills (14) 0.336 *
Central Great Plains (29) 0.201
W. High Plains (13) 0.128
Interior River Valleys and Hills (7) 0.16
Bailey Sections
Osage Plains (14) 0.228
South-Central Great Plains (31) 0.207
Ozark Highlands (16) 0.158
Nebraska Sand Hills (9) 0.124
North-Cent. Glaciated Plains (27) 0.259
N. Cent. US. Drift. &Escarp. Sect. (12) 0.212
MN &NE IA Morainal, Oak Sav. (21) 0.311
Flint Hills (17) 0.335 *
Central Loess Plains (8) 0.263
Central High Tablelands (7) 0.147
Central High Plains (6) 0.175
Central Dissected Till Plains (51) 0.189
4 Digit HUCs
Upper Missi.-Maquoketa-Plum (18) 0.236
Upper Missi-IA-Skunk-Wapsip. (32) 0.258
Republican (8) 0.123
Platte (6) 0.212
Niobrara (9) 0.111
Neosho-Verdigris (16) 0.216
Arkansas-Keystone (12) 0.236
Missouri-Nishnabotna (13) 0.255
Missouri-Little Sioux (11) 0.239
Middle Arkansas (9) 0.273
Lower Missouri (5) 0.199
Loup (7) 0.167
Kansas (13) 0.258
Gasconade-Osage (16) 0.172
Des Moines (19) 0.282 *
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
Within Group Bray-Curtis Similarity
Maxwell River Basins
a2b01 (22) 0.181
a2e01 (26) 0.243
a2d07 (15) 0.264
a2d06 (26) 0.172
a2d05 (33) 0.143
a2d04 (12) 0.243
a2b03 (16) 0.216
a2a28 (26) 0.173
a2a27 (9) 0.242
a2a26 (19) 0.285 *
a2a25 (19) 0.282
Small Geographic Distance Clusters
8 (11) 0.198
7 (13) 0.177
6 (19) 0.252
5 (17) 0.238
4 (41) 0.215
3 (32) 0.263 *
2 (22) 0.237
1 (10) 0.138
Stream Orders
5th (17) 0.241 *
4th (15) 0.186
3rd (26) 0.117
2nd (20) 0.129
1st (30) 0.13
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
Within Group Bray-Curtis Similarity

Figure 8. Similarity Dendrograms showing within-group Bray-Curtis similarities (W_i) for 6 classifications. The base of the dendrogram is located at the mean among-group similarity value (B) for the classification. The value shown at the end of the branches is the mean within-group similarity for the designated group or region (W_i). The longest branch of the dendrogram indicates the subregion or group with the most unique fish community, and the length of each branch is equal to $W_i – B$. This value represents a group's individual Classification Strength (CS). According to the dendrograms, the south central region of the study area (e.g., the Flint Hills) and northeastern Iowa generally have the highest within-region similarity among stream fish communities and the most unique fish assemblages.

Appendix for Chapter 1

Characteristic Fish Communities of Omernik Level III Ecoregions in Kansas, Missouri, Nebraska and Iowa

Reference stream fish communities in the Flint Hills are characterized by the presence of the widespread species listed in Table 7. Those species that are distinctive and widespread within the Flint Hills include: the stonecat (*Noturus flavus),* channel catfish *(Ictalurus punctatus),* longear sunfish (*Lepomis megalotis),* logperch *(Percina caprodes),* orangespotted sunfish *(Lepomis Humilis),* suckermouth minnow *(Phenacobius mirabiles)* and flathead catfish *(Pylodictis olivaris)* and distinguish the Flint Hills communities from other regions in the study area.

Fishes that are unique to the Flint Hills (see Table 8) reference streams compared to the other ecoregions studied here include: the brindled madtom (*Noturus miurus*) – though it has been found in Missouri and farther east in the past (Page and Burr 1991); the mimic shiner (*Notropis Volucellus*) - but has also been found in other studies in Missouri and to the east (Page and Burr 1991); and the slim minnow (*Pimephales tennellus*) – also found in Missouri (Page and Burr 1991). Those that are rare and somewhat restricted (rsr) to the Flint Hills (meaning they occur in at most two streams outside the ecoregion) include: the cardinal shiner (*Luxilus cardinalis*); the spotted sucker (*Minytrema melanops*), which is "in need of conservation;" the freckled madtom (*Noturus nocturnus*); the tiny ghost shiner (*Notropis buchanani*); and the channel darter (*Percina copelandi).*

Distinctive widespread species in the Driftless Area include: the fantail darter (*Etheostoma flabellare*) – this is the western edge of its range according to Page and Burr (1991); and the longnose dace (*Rhinichthys cataractae)* (see Table 7 for the complete list of widespread species in the Driftless Area).

The Driftless Area regionally unique species include: the slimy sculpin *(Cottus cognatus),* the burbot *(Lota lota)* – although it's been found by others in parts of Missouri, Kansas and Nebraska as well (Page and Burr 1991), the river shiner *(Notropis blennius)* – also has occurred in Missouri, Nebraska, Kansas and other parts of Iowa, the channel shiner *(Notropis Wickliffi)* and brook trout *(Salvelinus fontinalis)* – also found as an introduced species in Nebraska (Page and Burr 1991). The mottled sculpin (*Cottus bairdi*) and the mud darter (*Etheostoma asprigene)* were found to be rare and somewhat restricted to the Driftless Area.

The slender madtom (*Noturus exilis*) is the distinctive widespread species in the Ozark Highlands (see Table 7). The species that were found to be unique to this region (see table 8) are: the ozark sculpin (*Cottus hypselurus),* whitetail shiner *(Cyprinella galactura),* stippled darter (*Etheostoma punctulatum),* speckled darter (*Etheostoma stigmaeum),* Missouri saddled darter (*Etheostoma tetrazonum),* northern studfish (*Fundulus catenatus),* duskystripe shiner (*Luxilus pilsbryi),* the bleeding shiner (*Luxilus zonatus),* wedgespot shiner (*Notropis greenei),* telescope shiner (*Notropis telescopus)*, Ozark madtom (*Noturus albater),* and redspot chub (*Nocomis asper).* The greenside darter (*Etheostoma blennioides),* striped shiner

(*Luxilus chrysocephalus),* warmouth (*Lepomis gulosus),* cardinal shiner (*Luxilus cardinalis)* and banded sculpin (*Cottus carolinae)* are considered rare and somewhat restricted to the Ozark Highlands. The Ozark Highlands contains the largest number of unique species of all the regions studied here (12 species), followed closely by the Western Cornbelt Plains (11 unique species).

The Western Cornbelt Plains contains the bigmouth shiner (*Notropis dorsalis*) as its distinctive widespread species (Table 7). This ecoregion houses the following unique species (Table 8): spotfin shiner (*Cyprinella spiloptera);* blacknose dace *(Rhinichthys atratulus);* Mississippi silvery minnow *(Hybognathus nuchalis);* American brook lamprey (*Lampetra appendix)* – uncommon; the silver chub (*Macrhybopsis storeriana);* yellow perch (*Perca flavescens);* sauger (*Stizostedion canadense);* central mudminnow (*Umbra limi);* bowfin (*Amia calva);* goldfish (*Carassius auratus)* – exotic; and highfin carpsucker (*Carpiodes velifer)* – uncommon. The species that are rare and somewhat restricted to the Western Cornbelt Plains include: the grass pickerel (*Esox americanus);* northern pike (*Esox lucius)*- although abundant to the north; mud darter (*Etheostoma asprigene);* rainbow darter (*Etheostoma caeruleum);* Iowa darter *(Etheostoma exile);* goldeye (*Hiodon alosoides);* bigmouth shiner *(Hybopsis dorsalis);* plains minnow (*Hybognathus placitus)*- a species in need of conservation in Kansas (Cross and Collins 1995), which is also found in the Central Great Plains; pumpkinseed (*Lepomis gibbosus);* silver redhorse (*Moxostoma anisurum);* tadpole madtom (*Noturus gyrinus)* – in need of conservation in Kansas*;* flathead chub (*Platygobio gracilis);* and the walleye *(Stizostedion vitreum).* The Western Cornbelt Plains has more rare and somewhat restricted species than any other region in the study area.

The yellow bullhead *(Ameiurus Natalis)* is the lone distinctive widespread species for the Interior River Valleys and Hills, although the ecoregion has a large number of widespread species (11) - second only to the Flint Hills region (14 widespread species) (Table 8). The blacknose shiner (*Notropis heterolepis*) is the only unique species that was found within this ecoregion (Table 7), but this result could be due to the fact that a smaller proportion of the ecoregion was included in the analysis compared to other ecoregions in this study. The blacknose shiner is disappearing from its southern range (in Kansas and Missouri – Page and Burr 1991). The bigeye shiner (*Notropis boops*) is the only rare and somewhat restricted species found in the Interior River Valleys and Hills (Table 8).

The Western High Plains, Central Irregular Plains, Central Great Plains and Nebraska Sandhills are the four ecoregions with no distinctive widespread species (Table 7). The widespread species of the Central Irregular Plains reference streams include: the green sunfish (*Lepomis cyanellus*); largemouth bass *(Micropterus salmoides);* the bluntnose minnow *(Pimephales notatus);* the central stoneroller *(Campostoma anomalum);* the red shiner *(Cyprinella lutrensis),* blue gill *(Lepomis macrochirus),* and orange-throat darter *(Etheostoma spectabile)* (Table 7). This assemblage of widespread species are also found among the widespread species listed for the Interior River Valleys and Hills, and most of these widespread species are also found within the Flint Hills widespread species list as well.

The unique fishes of the Central Irregular Plains include: the river darter *(Percina shumardi*), which was found only in the Neosho river and is a "species in need of conservation" (Cross and Collins 1995); the trout perch (*Percopsis omiscomaycus)*; the blue sucker (*Cycleptus elongatus*) – numbers are declining (Page and Burr 1991); the bluntnose shiner (*Etheostoma chlorosomum*) – a species in need of conservation (Cross and Collins 1995); redfin darter (*Etheostoma whipplei*) - very small overall range; the redear sunfish (*Lepomis microlophus*); and inland silverside (*Menidia beryllina*) (Table 8). The rare and somewhat restricted species of the Central Irregular Plains are: the black buffalo (*Ictiobus niger)* - uncommon throughout its range; the greenside darter (*Etheostoma blennioides);* warmouth (*Lepomis gulosus*); spotted sucker (*Minytrema melanops*); ghost shiner (*Notropis buchanani);* and freckled madtom (*Noturus nocturnus*). The shortnose gar (*Lepisosteus platostomus)* is a special case, and was only found in one stream in the Central Irregular Plains and one stream in the Central Great Plains. This rarity is most likely due to the focus of sampling for this research on smaller stream habitats.

As mentioned above, there were no distinctive widespread species in the Western High Plains, but there were two unique species - the red river shiner (*Notropis bairdi* – an introduced species in Kansas which is replacing the Arkansas darter), and the Longnose sucker (*Catostomus catostomus*) – a cold water species (Table 8). The brassy minnow (*Hybognathus hankinsoni*) is rare and somewhat restricted to the Western High Plains among the ecoregions included in this analysis. This is a species in need of conservation in Kansas (Cross and Collins 1995), which is the southern edge of its range.

The Nebraska Sandhills contain two unique species – the finescale dace *(Phoxinus neogaeus* - listed as threatened in Nebraska) and the pearl dace (*Margariscus margarita),* which is part of an isolated population in this part of the Missouri river basin and is considered "vulnerable" by Natuserve. The northern redbelly dace (*Phoxinus eos*) is rare and somewhat restricted to the Nebraska sandhills (representing the southern limit of its range) among the ecoregions included in this study. The Nebraska Sand Hills share its other rare and somewhat restricted species with the Western Cornbelt Plains, and these include: the grass pickerel *(Esox americanus*) (present in two streams in each of the ecoregions); tadpole madtom (*Noturus gyrinus)* – present in only one stream in the Nebraska Sand Hills and two streams in the Western Cornbelt Plains; and the pumpkinseed (*Lepomis gibbosus),* which is found in one stream in each of three ecoregions (the Western Cornbelt Plains, Nebraska Sandhills,and the Driftless Area).

The unique species of the Central Great Plains reference streams are: the speckled chub (*Macrhybopsis aestivalis* – endangered in Kansas) and the white perch (*Morone americana*), which is an introduced species that is more often present in impoundments. Rare and somewhat restricted species for the Central Great Plains ecoergion are: the Arkansas darter (*Etheostoma cragini*) – a threatened species in Kansas, the plains killifish (*Fundulus zebrinus*), the goldeye (*Hiodon alosoides*), the bigmouth shiner (*Hybopsis dorsalis*), the plains minnow (*Hybognathus placitus*), which is a species in need of conservation in Kansas and is also found in a similar number of streams in the Western Cornbelt Plains; and the southern redbelly dace (*Phoxinus erythrogaster*). The shortnose gar *(Lepisosteus platostomus*) was mentioned previously as a special case due to its appearance only in one stream in the Central Great Plains and one in the Central Irregular Plains - again, likely due to the focus of this research on smaller rivers and streams.

The endangered Topeka shiner (*Notropis topeka*) was not restricted to one ecoregion, but was found in a few streams in the Cornbelt plains, Western High Plains, and the Flint Hills ecoregions.

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Appendix for Chapter 1
Appendix Tables A through D

		Sorensen Similarities (Presence/Absence)						**Bray-Curtis Similarities (Relative Abundance)**				
Small Group Name	No. of Groups	No. of Streams	Overall mean similarity within groups (W)	Mean similarity among groups (B)	Class. Strength (CS)%	B/W	% of maximum attainable CS	Overall mean similarity within groups (W)	Mean similarity among groups (B)	Class. Strength (CS)%	B/W	% of maximum attainable CS
Omernik Level III	9	210	0.46	0.29	18	0.62	75	0.21	0.11	10	0.51	57
Bailey Sections	12	223	0.49	0.30	19	0.62	75	0.22	0.12	11	0.52	55
Maxwell River Basins	11	223	0.48	0.32	16	0.66	69	0.21	0.12	9	0.58	50
Geographic Distance Clusters	8	165	0.50	0.30	20	0.60	79	0.23	0.12	11	0.51	43
4 digit HUCs	15	196	0.51	0.32	18	0.64	73	0.23	0.13	10	0.56	48
Strahler Order	5	115	0.36	0.29	7	0.81	30	0.15	0.11	4	0.74	27
Omernik Fish Clusters	9	210	0.51	0.28	23	0.54		0.27	0.10	18	0.36	
Bailey Fish Clusters	12	223	0.54	0.29	25	0.54		0.30	0.11	19	0.35	
Maxwell Fish Clusters	11	223	0.52	0.29	23	0.55		0.29	0.11	18	0.37	
Geog. Distance Fish Clusters	8	165	0.52	0.27	26	0.51		0.28	0.10	17	0.38	

HUC 4 Fish Clusters	15	196	0.56	0.32	25	0.56		0.32	0.11	21	0.34	
Strahler Order Fish Clusters	5	115	0.46	0.24	22	0.52		0.23	0.08	15	0.36	

Table A. Mean similarity values and classification strengths for smaller stream classification subdivisions, including the taxonomic fish clusters. The permutation tests for all a priori frameworks based on random site reassignments yielded a $p<0.000001$, indicating that the hypothesis of "no classification structure" was rejected. The % of maximum attainable CS is the CS of the framework as a percentage of the maximum possible CS value (based on the taxonomic fish clusters highlighted in yellow). The B/W ratios also indicate the strength of a classification scheme; a larger value close to 1 indicates a classification with no inherent value in accounting for stream variability (possible values are from 0 to 1).

Large Group Name	No. of Groups	No. of Streams	Overall mean similarity within groups (W)	Mean similarity among groups (B)	Class. Strength (CS)%	B/W	% of maximum attainable CS	Overall mean similarity within groups (W)	Mean similarity among groups (B)	Class. Strength (CS)%	B/W	% of maximum attainable CS
Maxwell Subregions	4	231	0.43	0.28	15	0.66	83	0.18	0.11	8	0.58	69
Geographic Distance Clusters	4	219	0.42	0.29	14	0.68	82	0.18	0.11	8	0.58	69
Omernik Level II	5	228	0.40	0.27	13	0.67	70	0.17	0.10	7	0.58	60
2 digit HUCs	3	231	0.39	0.29	11	0.73	55	0.16	0.11	6	0.66	61
Bailey Provinces	4	231	0.38	0.27	11	0.71	63	0.16	0.11	5	0.67	47
Strahler Order	5	115	0.36	0.29	7	0.81	30	0.15	0.11	4	0.74	27
Maxwell Fish Clusters	4	231	0.43	0.25	18	0.59		0.20	0.09	11	0.45	
Geographic Distance Fish Clusters	4	219	0.43	0.26	17	0.61		0.21	0.10	11	0.46	
Omernik Fish Clusters	5	228	0.44	0.25	19	0.57		0.21	0.09	12	0.43	
HUC 2 Fish Clusters	3	231	0.38	0.19	19	0.50		0.19	0.09	9	0.51	
Bailey Fish Clusters	4	231	0.43	0.25	18	0.59		0.20	0.09	11	0.45	
Strahler Order Fish Clusters	5	115	0.46	0.24	22	0.52		0.23	0.08	15	0.36	

Table B. Mean similarity values and classification strengths for larger stream classification subdivisions, including the taxonomic fish clusters. The permutation tests for all a priori frameworks based on random site reassignments yielded a $p<0.000001$, indicating that the hypothesis of “no classification structure” was rejected. The % of maximum attainable CS is the CS of the framework as a percentage of the maximum possible CS value (based on the taxonomic fish clusters highlighted in yellow). The B/W ratios also indicate the strength of a classification scheme; a larger value close to one indicates a classification with no inherent value in accounting for stream variability possible values are from 0 to 1)

Table C. Rank stream occupancy data for reference stream fish species in Omernik level III ecoregions of Kansas, Nebraska, Missouri and Iowa.

Western High Plains (n=13)			Central Great Plains (n=29)			Flint Hills (n=14)		
Species	No. of streams occupied	% of streams occupied	Species	No. of streams occupied	% of streams occupied	Species	No. of streams occupied	% of streams occupied
SEMOAT	10	77	PIMEPR	26	90	CAMPAN	14	100
PIMEPR	9	69	CYPRLU	25	86	CYPRLU	14	100
CATOCO	7	54	NOTRST	24	83	ETHESP	14	100
CAMPAN	4	31	LEPOCY	22	76	PIMENO	14	100
CYPRCA	4	31	CYPRCA	18	62	ICTAPU	13	93
CYPRLU	4	31	ICTAPU	16	55	LEPOCY	13	93
NOTRST	4	31	SEMOAT	15	52	PHENMI	13	93
SALMTR	4	31	CAMPAN	13	45	LEPOME	12	86
ETHESP	3	23	AMEIME	12	41	PERCCA	12	86
FUNDZE	3	23	CARPCA	12	41	LEPOHU	11	79
LEPOCY	3	23	PHENMI	12	41	MICRSA	11	79
ONCOMY	3	23	MICRSA	11	38	LYTHUM	10	71
RHINCA	3	23	AMEINA	10	34	NOTUFL	10	71
FUNDSC	2	15	GAMBAF	9	31	PYLOOL	10	71
HYBOHA	2	15	ETHESP	8	28	MOXOMA	9	64
LEPOHU	2	15	FUNDZE	8	28	LEPOMA	8	57
MICRSA	2	15	PYLOOL	8	28	MICRPU	8	57
AMEIME	1	8	CATOCO	6	21	PERCCO	8	57
CARPCY	1	8	DOROCE	6	21	PERCPH	8	57
CATOCA	1	8	PIMENO	6	21	PIMETE	8	57
ETHECR	1	8	PIMEVI	6	21	CYPRCM	7	50
GAMBAF	1	8	LEPOHU	5	17	MOXOER	7	50
ICTAPU	1	8	NOTRDO	5	17	NOTRRU	7	50
LEPOMA	1	8	APLOGR	4	14	AMEINA	6	43
MOROCH	1	8	ETHECR	4	14	FUNDNO	6	43
MOXOMA	1	8	CARPCY	3	10	GAMBAF	6	43
NOTRBA	1	8	HYBOPL	3	10	LEPIOS	6	43
NOTRDO	1	8	LEPOMA	3	10	NOTRST	6	43
NOTRTO	1	8	LEPOME	3	10	SEMOAT	6	43
PHENMI	1	8	MOXOMA	3	10	CYPRCA	5	36
POMONI	1	8	NOTECR	3	10	LABISI	5	36
ACIPFU	0		NOTRAT	3	10	LUXICO	5	36
ALOSCH	0		POMOAN	3	10	NOTRVO	5	36
ALOSPS	0		CYPRCM	2	7	PIMEPR	5	36
AMBLRU	0		HIODAL	2	7	CARPCA	4	29
AMEINA	0		HYBOHA	2	7	DOROCE	4	29
AMEINE	0		LABISI	2	7	ICTIBU	4	29
AMIACA	0		LEPIOS	2	7	PIMEVI	4	29
ANGROS	0		MACRAE	2	7	APLOGR	3	21
APHRSA	0		MOROCH	2	7	ETHEFL	3	21
APLOGR	0		NOTUFL	2	7	ETHENI	3	21
CAMPOL	0		HYBDOR	1	3	LUXICA	3	21

Table C. Rank stream occupancy data for reference stream fish species in Omernik level III ecoregions of Kansas, Nebraska, Missouri and Iowa.

Western High Plains (n=13)			Central Great Plains (n=29)			Flint Hills (n=14)		
Species	No. of streams occupied	% of streams occupied	Species	No. of streams occupied	% of streams occupied	Species	No. of streams occupied	% of streams occupied
CARAAU	0		ICTIBU	1	3	NOTUEX	3	21
CARPCA	0		ICTICY	1	3	POMOAN	3	21
CARVEL	0		LEPIPL	1	3	CATOCO	2	14
CATPLA	0		LUXICO	1	3	ICTINI	2	14
CENTMA	0		MICRPU	1	3	MINYME	2	14
COTTBA	0		MOROAM	1	3	MOROCH	2	14
COTTCA	0		PERCPH	1	3	NOTMIU	2	14
COTTCO	0		PHOXEO	1	3	NOTRBO	2	14
COTTHY	0		PLATGR	1	3	NOTRTO	2	14
COUPLU	0		POMONI	1	3	NOTUNO	2	14
CTENID	0		ACIPFU	0		AMEIME	1	7
CULAIN	0		ALOSCH	0		ICTICY	1	7
CYCELO	0		ALOSPS	0		NOTECR	1	7
CYPRCM	0		AMBLRU	0		NOTRBU	1	7
CYPRGA	0		AMEINE	0		PERCMA	1	7
CYPRSP	0		AMIACA	0		ACIPFU	0	
CYPRVE	0		ANGROS	0		ALOSCH	0	

Table C (cont'd). Rank stream occupancy data for reference stream fish species in Omernik level III ecoregions of Kansas, Nebraska, Missouri and Iowa.

Ozark Highlands (n=16)			**Central Irreg. Plains (n=21)**			**Neb. Sand Hills (n=10)**		
Species	No. of streams occupied	% of streams occupied	Species	No. of streams occupied	% of streams occupied	Species	No. of streams occupied	% of streams occupied
CAMPAN	15	94	CAMPAN	20	95	PIMEPR	8	80
LEPOCY	14	88	LEPOCY	20	95	CATOCO	7	70
LEPOMA	13	81	MICRSA	20	95	NOTRDO	6	60
NOTUEX	12	75	PIMENO	20	95	NOTRST	6	60
CAMPOL	10	63	CYPRLU	18	86	RHINCA	6	60
ETHECA	10	63	LEPOMA	18	86	CYPRLU	5	50
LEPOME	10	63	ETHESP	16	76	FUNDSC	5	50
LUXIZO	10	63	LEPOHU	13	62	SEMOAT	5	50
NOTRNU	10	63	LYTHUM	13	62	CYPRCA	4	40
COTTCA	9	56	PHENMI	13	62	LEPOMA	4	40
COTTHY	9	56	ICTAPU	12	57	MOXOMA	3	30
MICRDO	9	56	AMEINA	11	52	AMBLRU	2	20
SEMOAT	9	56	CYPRCA	11	52	AMEIME	2	20
ETHEFL	8	50	LABISI	10	48	ESOXAM	2	20
FUNDCA	8	50	LEPOME	10	48	HYBOHA	2	20
HYPENI	8	50	NOTRST	10	48	ICTAPU	2	20
NOCOBI	8	50	POMOAN	10	48	LEPOCY	2	20
AMBLRU	7	44	NOTUFL	9	43	NOTUFL	2	20
ETHESP	7	44	PERCCA	9	43	PHOXNE	2	20
FUNDOL	6	38	DOROCE	8	38	SALMTR	2	20
LUXICH	6	38	FUNDNO	8	38	AMEINA	1	10
MICRSA	6	38	NOTUEX	8	38	CULAIN	1	10
PHOXER	5	31	PERCPH	8	38	ESOXLU	1	10
AMEINA	4	25	PYLOOL	8	38	ETHEEX	1	10
ETHEBL	4	25	SEMOAT	8	38	LEPOGI	1	10
FUNDSC	4	25	CARPCA	7	33	LEPOHU	1	10
ETHEPU	3	19	PIMEVI	7	33	MARGMA	1	10
ETHEZO	3	19	ETHEFL	6	29	MICRSA	1	10
GAMBAF	3	19	LEPIOS	6	29	NOTECR	1	10
LUXIPI	3	19	MOXOER	6	29	NOTUGY	1	10
NOTUFL	3	19	APLOGR	5	24	ONCOMY	1	10
PERCCA	3	19	ETHENI	5	24	PHOXEO	1	10
CATOCO	2	13	GAMBAF	5	24	PIMENO	1	10
DOROCE	2	13	ICTIBU	5	24	PLATGR	1	10
ETHETE	2	13	NOTECR	5	24	POMOAN	1	10
LEPOGU	2	13	AMEIME	4	19	POMONI	1	10
MOXODU	2	13	CATOCO	4	19	STIZVI	1	10
MOXOER	2	13	MOROCH	4	19	ACIPFU	0	
NOTRAT	2	13	NOTRDO	4	19	ALOSCH	0	
NOTRGR	2	13	PIMEPR	4	19	ALOSPS	0	
NOTRRU	2	13	ETHEBL	3	14	AMEINE	0	
NOTRTE	2	13	ICTINI	3	14	AMIACA	0	

Table C (cont'd). Rank stream occupancy data for reference stream fish species in Omernik level III ecoregions of Kansas, Nebraska, Missouri and Iowa.

Ozark Highlands (n=16)			Central Irreg. Plains (n=21)			Neb. Sand Hills (n=10)		
Species	No. of streams occupied	% of streams occupied	Species	No. of streams occupied	% of streams occupied	Species	No. of streams occupied	% of streams occupied
NOTUAL	2	13	LEPOGU	3	14	ANGROS	0	
PIMENO	2	13	MICRPU	3	14	APHRSA	0	
APLOGR	1	6	MINYME	3	14	APLOGR	0	
COTTBA	1	6	MOXOMA	3	14	CAMPAN	0	
CYPRCA	1	6	NOTUNO	3	14	CAMPOL	0	
CYPRCM	1	6	CARPCY	2	10	CARAAU	0	
CYPRGA	1	6	CYPRCM	2	10	CARPCA	0	
CYPRLU	1	6	ETHCHL	2	10	CARPCY	0	
CYPRSP	1	6	LUXICO	2	10	CARVEL	0	
ERIMXP	1	6	MICRDO	2	10	CATOCA	0	
ETHEST	1	6	NOCOBI	2	10	CATPLA	0	
ICTAPU	1	6	NOTRAT	2	10	CENTMA	0	
LEPIOS	1	6	NOTRBU	2	10	COTTBA	0	
LUXICA	1	6	STIZVI	2	10	COTTCA	0	
MICRPU	1	6	CYCELO	1	5	COTTCO	0	
NOCOAS	1	6	ERIMXP	1	5	COTTHY	0	
NOTECR	1	6	ETHEWH	1	5	COUPLU	0	
NOTRBO	1	6	FUNDOL	1	5	CTENID	0	
ONCOMY	1	6	LEPIPL	1	5	CYCELO	0	
PERCCO	1	6	LEPOMI	1	5	CYPRCM	0	
POMOAN	1	6	MENBER	1	5	CYPRGA	0	
ACIPFU	0		NOTRVO	1	5	CYPRSP	0	
ALOSCH	0		PERCCO	1	5	CYPRVE	0	
ALOSPS	0		PEROMI	1	5	DOROCE	0	
AMEIME	0		PERSHU	1	5	DOROPE	0	
AMEINE	0		PIMETE	1	5	ERIMDI	0	
AMIACA	0		POMONI	1	5	ERIMOB	0	
ANGROS	0		ACIPFU	0		ERIMXP	0	

Table C (cont'd). Rank stream occupancy data for reference stream fish species in Omernik level III ecoregions of Kansas, Nebraska, Missouri and Iowa.

Western Corn Belt Plains (n=88)			Driftless Area (n=12)			Interior River Valleys and Hills (n=7)		
Species	No. of streams occupied	% of streams occupied	Species	No. of streams occupied	% of streams occupied	Species	No. of streams occupied	% of streams occupied
SEMOAT	80	91	CATOCO	11	92	AMEINA	7	100
NOTRST	78	89	ETHEFL	10	83	LEPOCY	7	100
NOTRDO	70	80	RHINCA	9	75	CAMPAN	6	86
LEPOCY	69	78	SEMOAT	9	75	LEPOMA	6	86
PIMEPR	64	73	CULAIN	7	58	LYTHUM	6	86
CATOCO	63	72	ETHENI	7	58	PIMENO	6	86
PIMENO	60	68	RHINAT	7	58	SEMOAT	6	86
ETHENI	58	66	SALMTR	7	58	CATOCO	5	71
CAMPAN	55	63	CAMPAN	6	50	CYPRLU	5	71
NOTUFL	55	63	LUXICO	5	42	ETHESP	5	71
LUXICO	53	60	NOCOBI	5	42	MICRSA	5	71
CYPRCA	47	53	ONCOMY	5	42	ETHENI	4	57
PHENMI	44	50	PIMENO	5	42	MOXOER	4	57
MOXOMA	41	47	PIMEPR	5	42	NOTRST	4	57
ICTAPU	40	45	COTTBA	4	33	DOROCE	3	43
CYPRLU	39	44	HYPENI	4	33	ETHEFL	3	43
AMEINA	37	42	LEPOCY	4	33	LABISI	3	43
CYPRSP	36	41	LOTLOT	4	33	NOTRBO	3	43
MICRSA	36	41	MOXOER	4	33	NOTRDO	3	43
LEPOMA	33	38	PHOXER	4	33	NOTUEX	3	43
ETHEFL	32	36	COTTCO	3	25	PERCCA	3	43
NOCOBI	32	36	MICRDO	3	25	PHENMI	3	43
MOXOER	31	35	MICRSA	3	25	CYPRCA	2	29
HYPENI	30	34	NOTRAT	3	25	FUNDNO	2	29
RHINAT	30	34	NOTRDO	3	25	FUNDOL	2	29
CARPCY	28	32	NOTRST	3	25	HYPENI	2	29
PERCMA	28	32	NOTUFL	3	25	LEPOHU	2	29
MICRDO	27	31	SALVFO	3	25	LEPOME	2	29
CARPCA	23	26	AMEINA	2	17	MICRDO	2	29
AMEIME	19	22	CYPRCA	2	17	MOXODU	2	29
HYBOHA	18	20	CYPRSP	2	17	NOTECR	2	29
NOTRRU	13	15	NOTRBL	2	17	POMOAN	2	29
ESOXLU	11	13	NOTRRU	2	17	AMEIME	1	14
ETHEZO	11	13	PERCMA	2	17	APLOGR	1	14
LEPOHU	11	13	PHENMI	2	17	CAMPOL	1	14
PERCPH	11	13	AMEIME	1	8	CARPCA	1	14
DOROCE	10	11	ERIMXP	1	8	COTTCA	1	14
AMBLRU	9	10	ETHASP	1	8	GAMBAF	1	14
CARVEL	9	10	ETHECA	1	8	ICTAPU	1	14
NOTRAT	9	10	ETHEZO	1	8	LUXICH	1	14
NOTUEX	9	10	HYBOHA	1	8	LUXICO	1	14

Table C (cont'd). Rank stream occupancy data for reference stream fish species in Omernik level III ecoregions of Kansas, Nebraska, Missouri and Iowa.

Western Corn Belt Plains (n=88)			Driftless Area (n=12)			Interior River Valleys and Hills (n=7)		
Species	No. of streams occupied	% of streams occupied	Species	No. of streams occupied	% of streams occupied	Species	No. of streams occupied	% of streams occupied
PHOXER	9	10	LEPOGI	1	8	MICRPU	1	14
MOXOAN	8	9	LEPOMA	1	8	MOXOAN	1	14
STIZVI	8	9	MOXODU	1	8	MOXOMA	1	14
ETHEEX	7	8	MOXOMA	1	8	NOTRHE	1	14
LAMAPP	7	8	NOTRWI	1	8	NOTRRU	1	14
PLATGR	7	8	PERCCA	1	8	PIMEPR	1	14
CULAIN	6	7	ACIPFU	0		PYLOOL	1	14
ICTICY	6	7	ALOSCH	0		ACIPFU	0	
POMOAN	6	7	ALOSPS	0		ALOSCH	0	
CAMPOL	5	6	AMBLRU	0		ALOSPS	0	
MOXODU	5	6	AMEINE	0		AMBLRU	0	
NOTRNU	5	6	AMIACA	0		AMEINE	0	
PERCCA	5	6	ANGROS	0		AMIACA	0	
APLOGR	4	5	APHRSA	0		ANGROS	0	
ETHECA	4	5	APLOGR	0		APHRSA	0	
ETHESP	4	5	CAMPOL	0		CARAAU	0	
PYLOOL	4	5	CARAAU	0		CARPCY	0	
HYBOPL	3	3	CARPCA	0		CARVEL	0	
LYTHUM	3	3	CARPCY	0		CATOCA	0	
MOROCH	3	3	CARVEL	0		CATPLA	0	
NOTUGY	3	3	CATOCA	0		CENTMA	0	
PERCFL	3	3	CATPLA	0		COTTBA	0	
POMONI	3	3	CENTMA	0		COTTCO	0	
RHINCA	3	3	COTTCA	0		COTTHY	0	
ESOXAM	2	2	COTTHY	0		COUPLU	0	
ETHASP	2	2	COUPLU	0		CTENID	0	
FUNDNO	2	2	CTENID	0		CULAIN	0	
HYBDOR	2	2	CYCELO	0		CYCELO	0	
HYBONU	2	2	CYPRCM	0		CYPRCM	0	
ICTIBU	2	2	CYPRGA	0		CYPRGA	0	
NOTECR	2	2	CYPRLU	0		CYPRSP	0	
UMBLIM	2	2	CYPRVE	0		CYPRVE	0	
AMIACA	1	1	DOROCE	0		DOROPE	0	
CARAAU	1	1	DOROPE	0		ERIMDI	0	
ERIMXP	1	1	ERIMDI	0		ERIMOB	0	
FUNDSC	1	1	ERIMOB	0		ERIMXP	0	
HIODAL	1	1	ESOXAM	0		ESOXAM	0	
LABISI	1	1	ESOXLU	0		ESOXLU	0	
LEPOGI	1	1	ESOXMA	0		ESOXMA	0	
MACRST	1	1	ESOXNI	0		ESOXNI	0	
NOTRTO	1	1	ETHCHL	0		ETHASP	0	
SALMTR	1	1	ETHEBL	0		ETHCHL	0	

Table C (cont'd). Rank stream occupancy data for reference stream fish species in Omernik level III ecoregions of Kansas, Nebraska, Missouri and Iowa.

Western Corn Belt Plains (n=88)			**Driftless Area (n=12)**			**Interior River Valleys and Hills (n=7)**		
Species	No. of streams occupied	% of streams occupied	Species	No. of streams occupied	% of streams occupied	Species	No. of streams occupied	% of streams occupied
STIZCA	1	1	ETHECR	0		ETHEBL	0	
ACIPFU	0		ETHEEU	0		ETHECA	0	

Table D. Code names and scientific names for 142 fish species found to be present in Nebraska, Kansas, Missouri and Iowa reference streams studied here

Species Code	Species Scientific Name	Species Code	Species Scientific Name
AMBLRU	*AMBLOPLITES RUPESTRIS*	FUNDOL	*FUNDULUS OLIVACEUS*
AMEIME	*AMEIURUS MELAS*	FUNDSC	*FUNDULUS SCIADICUS*
AMEINA	*AMEIURUS NATALIS*	FUNDZE	*FUNDULUS ZEBRINUS*
AMIACA	*AMIA CALVA*	GAMBAF	*GAMBUSIA AFFINIS*
APLOGR	*APLODINOTUS GRUNNIENS*	HIODAL	*HIODON ALOSOIDES*
CAMPAN	*CAMPOSTOMA ANOMALUM*	HYBDOR	*HYBOPSIS DORSALIS*
CAMPOL	*CAMPOSTOMA OLIGOLEPIS*	HYBOHA	*HYBOGNATHUS HANKINSONI*
CARAAU	*CARASSIUS AURATUS*	HYBONU	*HYBOGNATHUS NUCHALIS*
CARPCA	*CARPIODES CARPIO*	HYBOPL	*HYBOGNATHUS PLACITUS*
CARPCY	*CARPIODES CYPRINUS*	HYPENI	*HYPENTELIUM NIGRICANS*
CARVEL	*CARPIODES VELIFER*	ICTAPU	*ICTALURUS PUNCTATUS*
CATOCA	*CATOSTOMUS CATOSTOMUS*	ICTIBU	*ICTIOBUS BUBALUS*
CATOCO	*CATOSTOMUS COMMERSONI*	ICTICY	*ICTIOBUS CYPRINELLUS*
COTTBA	*COTTUS BAIRDI*	ICTINI	*ICTIOBUS NIGER*
COTTCA	*COTTUS CAROLINAE*	LABISI	*LABIDESTHES SICCULUS*
COTTCO	*COTTUS COGNATUS*	LAMAPP	*LAMPETRA APPENDIX*
COTTHY	*COTTUS HYPSELURUS*	LEPIOS	*LEPISOSTEUS OSSEUS*
CULAIN	*CULAEA INCONSTANS*	LEPIPL	*LEPISOSTEUS PLATOSTOMUS*
CYCELO	*CYCLEPTUS ELONGATUS*	LEPOCY	*LEPOMIS CYANELLUS*
CYPRCA	*CYPRINUS CARPIO*	LEPOGI	*LEPOMIS GIBBOSUS*
CYPRCM	*CYPRINELLA CAMURA*	LEPOGU	*LEPOMIS GULOSUS*
CYPRGA	*CYPRINELLA GALACTURA*	LEPOHU	*LEPOMIS HUMILIS*
CYPRLU	*CYPRINELLA LUTRENSIS*	LEPOMA	*LEPOMIS MACROCHIRUS*
CYPRSP	*CYPRINELLA SPILOPTERA*	LEPOME	*LEPOMIS MEGALOTIS*
DOROCE	*DOROSOMA CEPEDIANUM*	LEPOMI	*LEPOMIS MICROLOPHUS*
ERIMXP	*ERIMYSTAX X-PUNCTATUS*	LOTLOT	*LOTA LOTA*
ESOXAM	*ESOX AMERICANUS*	LUXICA	*LUXILUS CARDINALIS*
ESOXLU	*ESOX LUCIUS*	LUXICH	*LUXILUS CHRYSOCEPHALUS*
ETHASP	*ETHEOSTOMA ASPRIGENE*	LUXICO	*LUXILUS CORNUTUS*
ETHCHL	*ETHEOSTOMA CHLOROSOMUM*	LUXIPI	*LUXILUS PILSBRYI*
ETHEBL	*ETHEOSTOMA BLENNIOIDES*	LUXIZO	*LUXILUS ZONATUS*
ETHECA	*ETHEOSTOMA CAERULEUM*	LYTHUM	*LYTHRURUS UMBRATILIS*
ETHECR	*ETHEOSTOMA CRAGINI*	MACRAE	*MACRHYBOPSIS AESTIVALIS*
ETHEEX	*ETHEOSTOMA EXILE*	MACRST	*MACRHYBOPSIS STORERIANA*
ETHEFL	*ETHEOSTOMA FLABELLARE*	MARGMA	*MARGARISCUS MARGARITA*
ETHENI	*ETHEOSTOMA NIGRUM*	MENBER	*MENIDIA BERYLLINA*
ETHEPU	*ETHEOSTOMA PUNCTULATUM*	MICRDO	*MICROPTERUS DOLOMIEU*
ETHESP	*ETHEOSTOMA SPECTABILE*	MICRPU	*MICROPTERUS PUNCTULATUS*
ETHEST	*ETHEOSTOMA STIGMAEUM*	MICRSA	*MICROPTERUS SALMOIDES*
ETHETE	*ETHEOSTOMA TETRAZONUM*	MINYME	*MINYTREMA MELANOPS*
ETHEWH	*ETHEOSTOMA WHIPPLEI*	MOROAM	*MORONE AMERICANA*
ETHEZO	*ETHEOSTOMA ZONALE*	MOROCH	*MORONE CHRYSOPS*
FUNDCA	*FUNDULUS CATENATUS*	MOXOAN	*MOXOSTOMA ANISURUM*
FUNDNO	*FUNDULUS NOTATUS*	MOXODU	*MOXOSTOMA DUQUESNEI*

Table D (Cont'd). Code names and scientific names for 142 fish species found to be present in Nebraska, Kansas, Missouri and Iowa reference streams studied here

MOXOER	*MOXOSTOMA ERYTHRURUM*
MOXOMA	*MOXOSTOMA MACROLEPIDOTUM*
NOCOAS	*NOCOMIS ASPER*
NOCOBI	*NOCOMIS BIGUTTATUS*
NOTECR	*NOTEMIGONUS CRYSOLEUCAS*
NOTMIU	*NOTURUS MIURUS*
NOTRAT	*NOTROPIS ATHERINOIDES*
NOTRBA	*NOTROPIS BAIRDI*
NOTRBL	*NOTROPIS BLENNIUS*
NOTRBO	*NOTROPIS BOOPS*
NOTRBU	*NOTROPIS BUCHANANI*
NOTRDO	*NOTROPIS DORSALIS*
NOTRGR	*NOTROPIS GREENEI*
NOTRHE	*NOTROPIS HETEROLEPIS*
NOTRNU	*NOTROPIS NUBILUS*
NOTRRU	*NOTROPIS RUBELLUS*
NOTRST	*NOTROPIS STRAMINEUS*
NOTRTE	*NOTROPIS TELESCOPUS*
NOTRTO	*NOTROPIS TOPEKA*
NOTRVO	*NOTROPIS VOLUCELLUS*
NOTRWI	*NOTROPIS WICKLIFFI*
NOTUAL	*NOTURUS ALBATER*
NOTUEX	*NOTURUS EXILIS*
NOTUFL	*NOTURUS FLAVUS*
NOTUGY	*NOTURUS GYRINUS*
NOTUNO	*NOTURUS NOCTURNUS*
ONCOMY	*ONCORHYNCHUS MYKISS*
PERCCA	*PERCINA CAPRODES*
PERCCO	*PERCINA COPELANDI*
PERCFL	*PERCA FLAVESCENS*
PERCMA	*PERCINA MACULATA*
PERCPH	*PERCINA PHOXOCEPHALA*
PEROMI	*PERCOPSIS OMISCOMAYCUS*
PERSHU	*PERCINA SHUMARDI*
PHENMI	*PHENACOBIUS MIRABILIS*
PHOXEO	*PHOXINUS EOS*
PHOXER	*PHOXINUS ERYTHROGASTER*
PHOXNE	*PHOXINUS NEOGAEUS*
PIMENO	*PIMEPHALES NOTATUS*
PIMEPR	*PIMEPHALES PROMELAS*
PIMETE	*PIMEPHALES TENELLUS*
PIMEVI	*PIMEPHALES VIGILAX*
PLATGR	*PLATYGOBIO GRACILIS*
POMOAN	*POMOXIS ANNULARIS*
POMONI	*POMOXIS NIGROMACULATUS*
PYLOOL	*PYLODICTIS OLIVARIS*
RHINAT	*RHINICHTHYS ATRATULUS*
RHINCA	*RHINICHTHYS CATARACTAE*
SALMTR	*SALMO TRUTTA*
SALVFO	*SALVELINUS FONTINALIS*
SEMOAT	*SEMOTILUS ATROMACULATUS*
STIZCA	*STIZOSTEDION CANADENSE*
STIZVI	*STIZOSTEDION VITREUM*
UMBLIM	*UMBRA LIMI*

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Appendix Figures A through E. Sorenson and Bray-Curtis taxonomic fish community clusters projected onto the various regional classification schemes at the finer scale used in this study. Good correspondence was not seen between taxonomic fish clusters and regional classificiation schemes.

Figure A. Bailey sections with 12 taxonomic fish clusters (Sorensen)

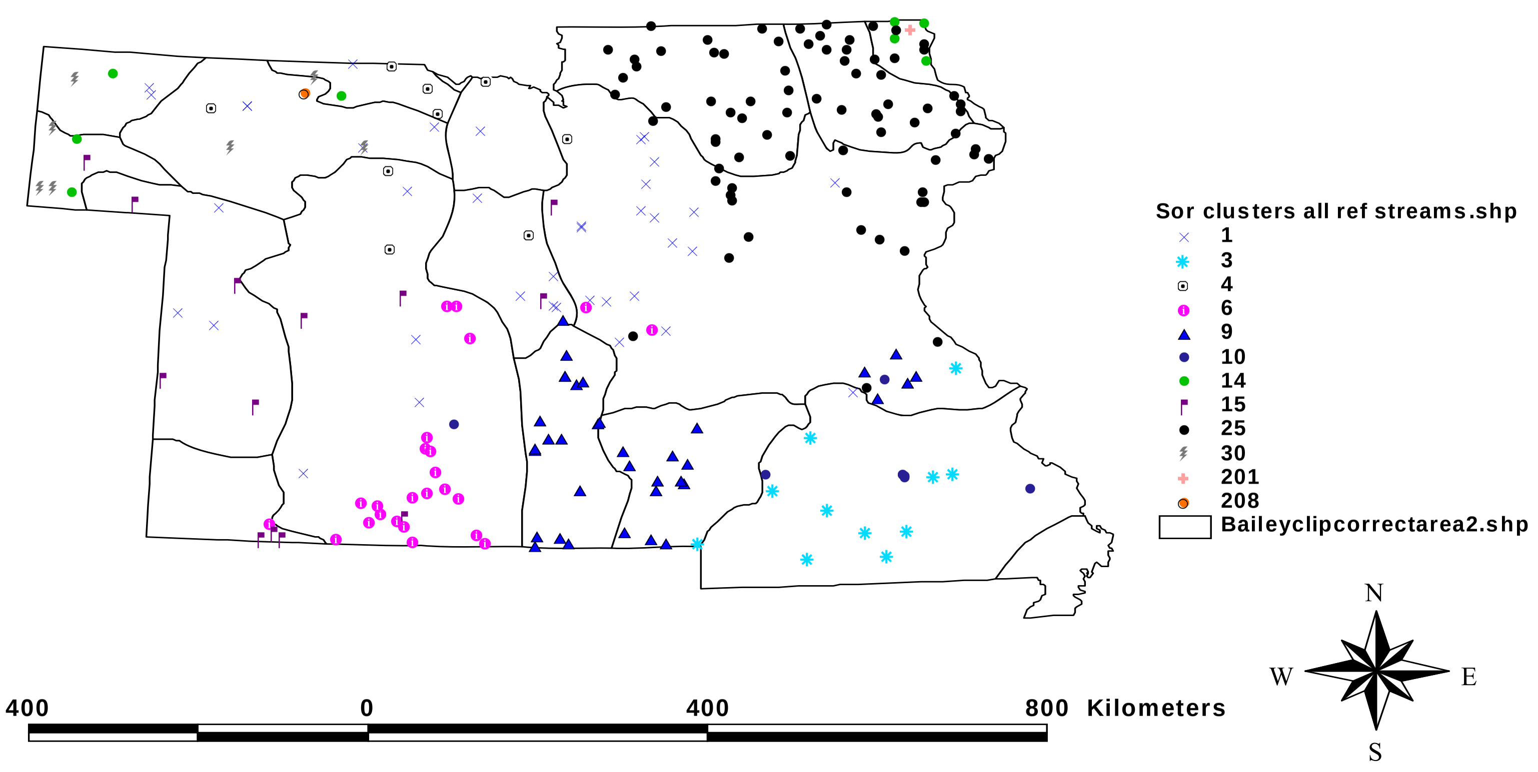


Figure B. Omernik level III with 12 fish clusters (Sorensen)

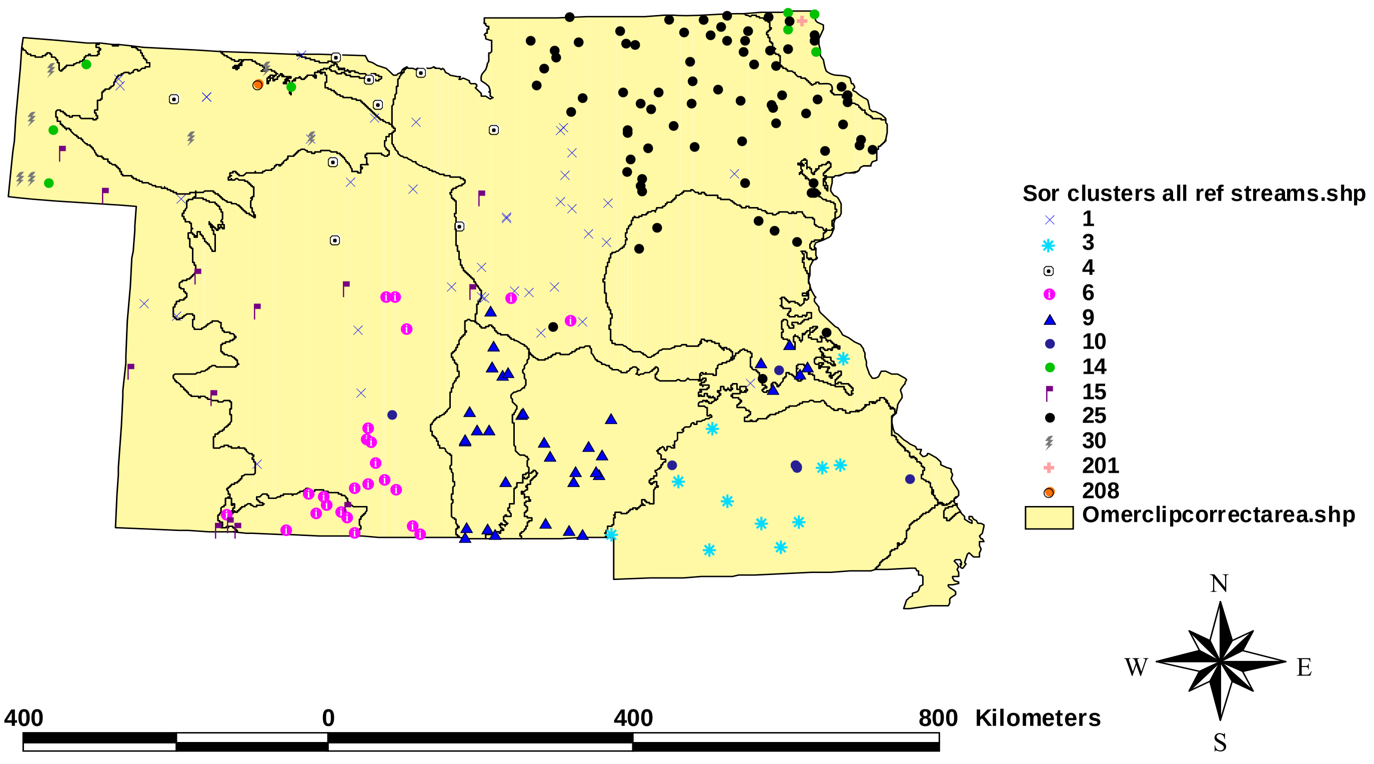


Figure C. Maxwell basins with 12 taxonomic fish clusters (Sorensen)

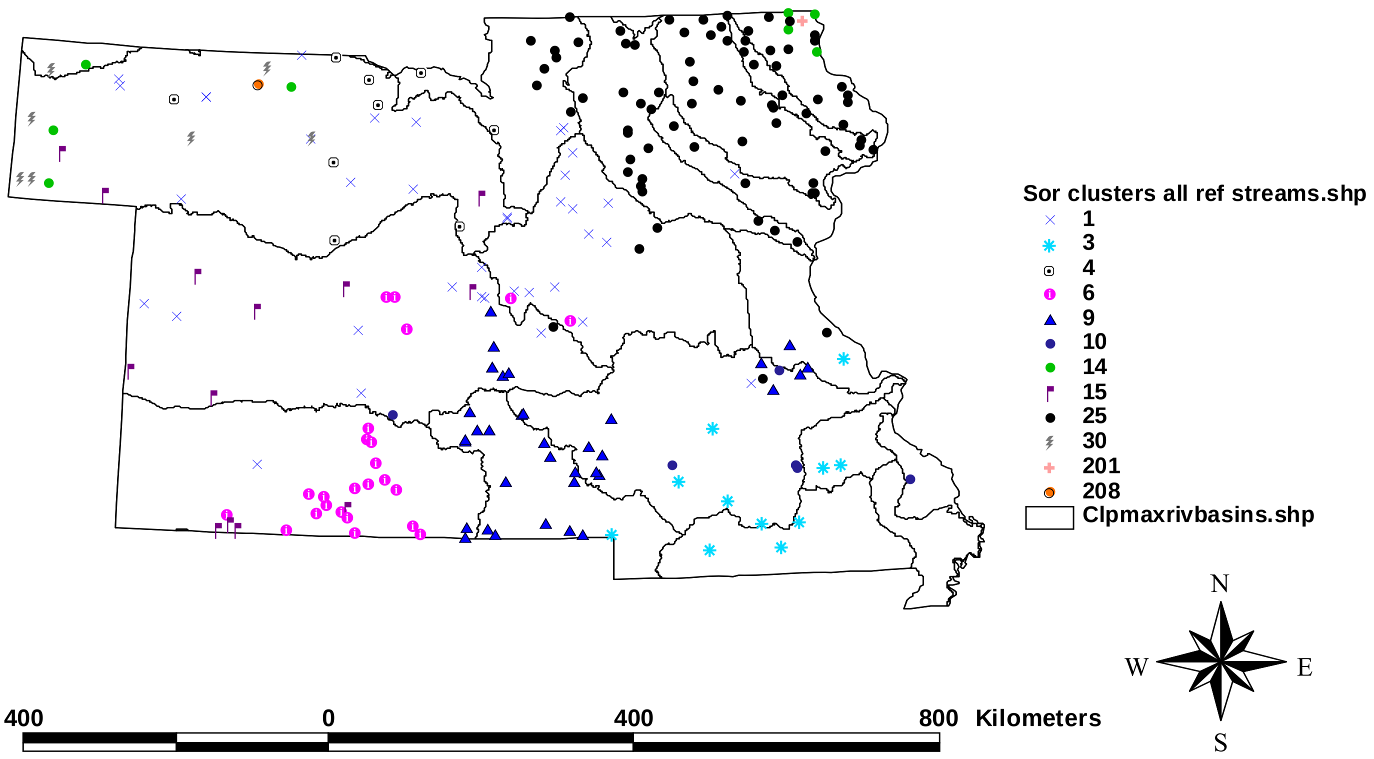
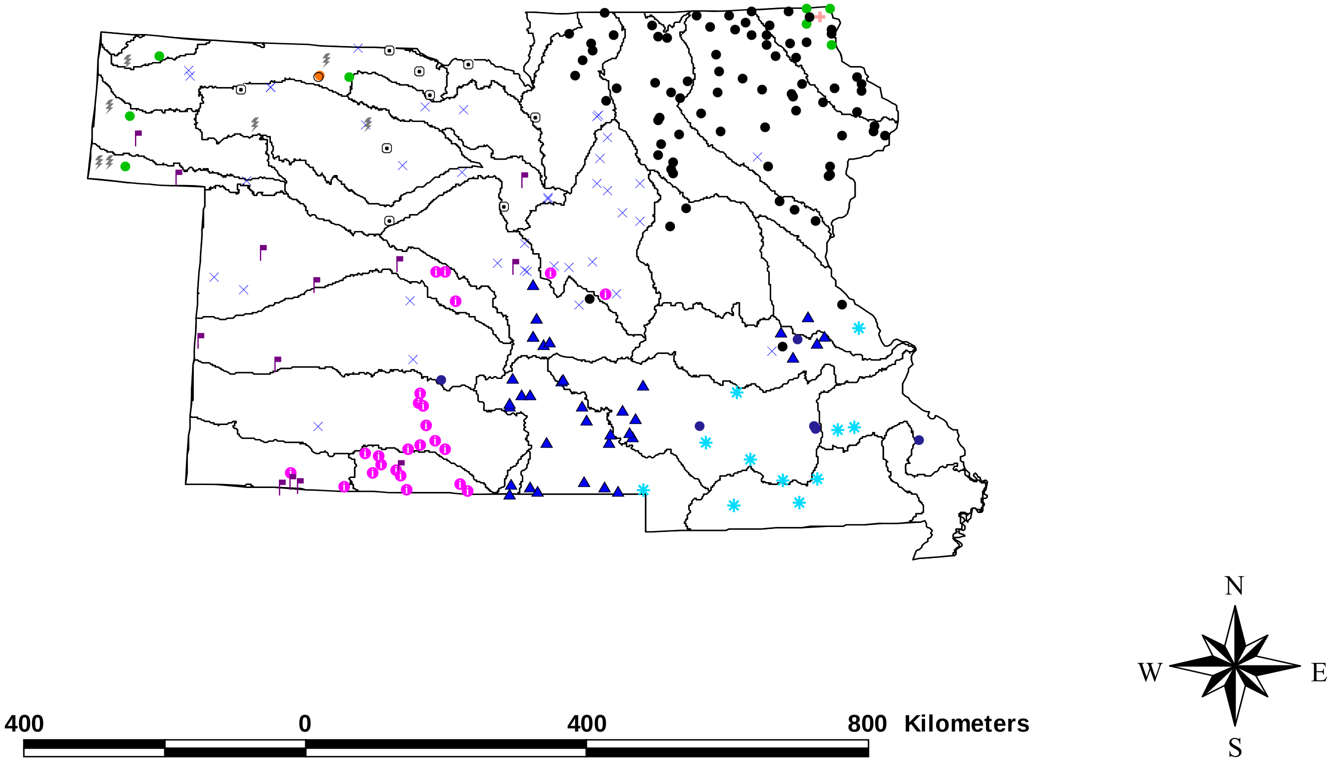
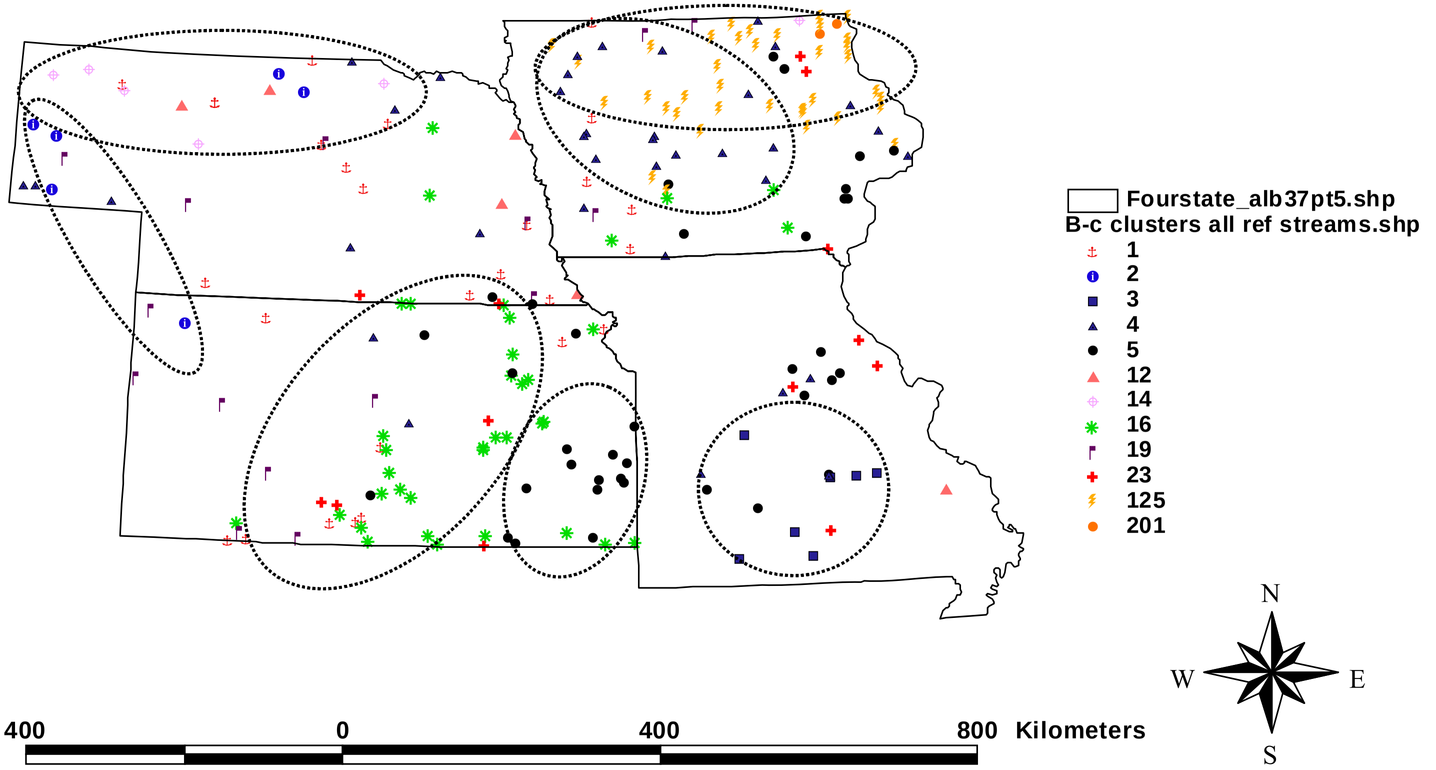


Figure D. 4 digit HUCs with 12 taxonomic fish clusters (Sorensen)



Taxonomically similar groups that clusterd geographically are circle

Figure E. Bray-Curtis taxonomic fish community clusters over the 4-state study area



CHAPTER TWO

A hybrid ecoregion/watershed stream classification framework for the Midwest: How do ecological and physical boundaries to dispersal interact to impact stream fish communities?

Introduction

In trying to account for ecosystem patterns at a coarse scale, there is much debate as to whether watersheds or ecoregions are a more appropriate tool to classify stream systems. Watersheds may be useful tools, because they represent physical and potentially longer-term historical barriers to dispersal of aquatic communities. Alternatively, ecoregions may be useful because they represent ecological barriers to dispersal, outside of which the habitat type will potentially change.

Omernik and Griffith (1991) and Omernik and Bailey (1997) discuss the debate regarding the utility of watersheds versus ecoregions to classify aquatic ecosystems. In both of the above manuscripts, the authors promote the use of both watersheds and ecoregions in some locations (in a complementary fashion) and just one of the classifications in other geographic locations. The preferred use of only one type of classification (ecoregions) is particularly suggested for very sandy areas, areas with little relief (such as much of the Midwest), and xeric areas. Currently, the US Geological Survey (USGS), the US Forest Service, the US Environmental Protection

Agency (USEPA) and many US state agencies are still using watersheds in some capacity, but quite a few states are delineating finer levels (i.e., level 4) of Omernik's hierarchical ecoregions (eg., Ohio, Kansas, Arkansas, Minnesota, and Oregon, Indiana, North and South Dakota, Montana, Utah, Missouri, and Iowa) to provide a regional basis for aquatic ecosystem monitoring.

The previous study discussed in Chapter One revealed that watersheds or HUCs (representing physical boundaries to dispersal) and ecoregions (representing ecological boundaries to dispersal) had a similarly high classification strength ranking based on patterns in fish community similarity across four states – Kansas, Missouri, Nebraska and Iowa (see Table 1). This indicates that these different types of dispersal boundaries may be equally important in shaping stream communities. To test the relative importance of these two types of barriers/influences on fish communities in this four-state area of the Midwest, a hybrid framework was constructed consisting of the two major ecoregion approaches of Bailey (Cleland et al. 1997) and Omernik (1995) stratified by HUC's (hydrological unit codes – Seaber et al. 1987). A classification strength (CS) analysis based on fish community similarity was then performed on these new hybrid regions. The extent to which the hybrid regions out-performed (or did not outperform) the unaltered HUC (watershed) and ecoregion classifications indicates the effectiveness of putting an equal weight on physical boundaries and ecological boundaries to dispersal in the design of stream classifications for the Midwest.

If the combination ecoregion/watershed design is found to have a higher CS than the ecoregion or watershed alone, this indicates that the watershed or ecoregion alone is not the most appropriate tool for explaining and predicting aquatic biota and that the interaction between hydrologic boundaries and ecological boundaries in shaping aquatic communities needs to be better accounted for in the regionalization process. Likely, the outcome will vary with the area under consideration. For example, a sandier area, drier area, or area of little relief would probably respond best to the ecoregion classification approach, while an area with high precipitation and more relief would probably be best delineated with a framework that relies more heavily on watershed boundaries. Therefore, an area like the Sand Hills of Nebraska may be described better using an ecoregion approach than a watershed approach or an approach that relies heavily on watershed boundaries (Maxwell et al. 1995).

To further understand what may be driving stream community patterns in the study area, a subset of data was analyzed using the same classification strength analysis as above, but the communities were broken into reproductive guilds (based on Balon's classifications - 1975) and adult functional feeding guilds rather than species. This way of describing fish community patterns may provide more information about the type of environmental factors shaping stream communities, because fish are grouped by ecological niche. Because reproductive guilds are based on the kind of environment or habitat in which eggs can develop, the occurrence of certain guild communities is likely to be closely linked with environmental factors that are most important to the survival of those fish. If this linkage is not seen in the analysis (i.e., if the classification strength of the hybrid ecoregion/watershed classification approach is less than the CS of the watershed approach), this may indicate that historical physical boundaries to dispersal may have a greater influence on modern-day fish communities.

The results of this study will potentially help to distinguish whether fish in the Midwest historically have been influenced more by physical dispersal limitations (i.e., topographical drainage boundaries) than ecological limitations (i.e., regions of different climate and land-cover), or whether these factors have an equally important impact. The literature addressing the relative influence of ecoregions vs. watersheds is not conclusive, and is beset by the use of different regional units that represent the watershed in different ways (i.e., the Hydrologic Unit Code (HUC) – also known as the Hydrologic accounting Unit (HAU), which is not always created based on topography). In Georgia, Feminella (2000) explored the complementarity of watersheds and ecoregions suggested by Omernik and Bailey (1997) by testing whether streams within a catchment/watershed (the Altamaha River catchment) that crossed two ecoregions would be more similar to each other based on ecoregion or based on catchment. After comparing stream invertebrate assemblages, he found that streams were more similar within the ecoregion than within the catchment that crossed the two ecoregions, indicating that ecoregions and watersheds are complementary. However, Feminella's sample size was quite small (4 streams total - 2 streams in each ecoregion). In Oregon, Van Sickle and Hughes (2000) attempted to combine the strengths of the watershed and ecoregion classifications by dividing the

Williamette Basin HAU (Hydrologic Accounting Unit or HUC) by Omernik level III ecoregions and creating a hybrid regional classification for streams. Their analysis, based on patterns in fish community similarity, suggested that this hybrid classification may be stronger than either the ecoregion or HAU alone when applied to streams. After surveying several studies comparing regional stream classifications, Hawkins et al. (2000) reported that smaller catchments or watersheds generally corresponded better with patterns in biotic variation in streams than ecoregions, but larger catchments (analogous to one and two digit HUCs) did not. However, four out of the eight ecoregion/watershed comparison studies that Hawkins et al. (2000) surveyed reported that ecoregions and watersheds have similar classification strengths.

This study compares fish community patterns across the states of Kansas, Nebraska, Iowa and Missouri. In this region of the Midwest, the strong indirect historical influence of glaciation on fish dispersal (mainly by its forcing of northern faunas into southern refugia) was supported by Cross et al. and Robison (in Hocutt and Wiley 1986). Robison also stated that the Kansas Flint Hills were a major Late Tertiary divide between drainages in the Great Plains. He emphasized research by Guillory (1978), who stated that dispersal of small stream fishes in the Mississippi basin historically was influenced by periods of pleistocene glaciation during which stream fishes dispersed down and across the Mississipi River and other rivers into southern refugia. Cross et al (in Hocutt and Wiley 1986) stated that ecological factors were more influential to fish distributions than drainage boundaries in much of the western Mississippi drainage, with the exception of parts of the Ozark Highlands. This observation was based on their finding that most fish species occupied parts of different drainage basins, and no one species was present throughout a single river drainage. Indeed, the fact that the study area for this work is not very topographically diverse, along with low levels of glaciation in this region (with the exception of more intense glacial activity in the Northeast portion of the study area), indicate that physical barriers to fish dispersal may be secondary in importance to ecological barriers.

Materials and Methods

Experimental design and classifications analyzed

As in the previous study (Chapter one), the study area spans most of Nebraska, Kansas, Iowa and Missouri. As in Chapter one, this was also a bioinformatics-based study that utilized disparate databases from government agencies across the extensive study area to assess the relative importance of physical boundaries to stream fish dispersal vs ecological boundaries to dispersal in this part of the Midwest. The relative importance of these two types of dispersal barriers for fish species was assessed by comparing the classification strength of the watershed or HUC classification approach for streams (representing physical boundaries to dispersal) to the ecoregion classification approaches (representing ecological boundaries to dispersal), and to classification approaches that are a hybrid of the ecoregion approach and the watershed approach. The classification strength (CS) analysis employed here is similar to the method described previously by Chapin et al. (in prep) and by Van Sickle and Hughes (2000), who used patterns in aquatic vertebrates to compare the ecological validity of stream classification approaches in Oregon.

The classification strength of five *a priori* regional classification approaches were assessed in regards to their ability to classify stream fish communities in order to examine the relative influence of different types of dispersal barriers. The *a priori* regional classifications included: 4-digit Hydrologic Unit Codes (HUCs) or watersheds; sections of Bailey's ecoregions; Omernik's level III ecoregions; and two hybrid regional classification approaches, which were constructed by stratifying both Bailey's provinces and Omernik's level two ecoregions by watersheds (2-digit HUCs). All of these classifications represent comparable scales (see Table 2 and Fig.s 1-5, as well as Fig.s 3-5 in Chapter one).

To put these five classification approaches into context, they were compared to two non-regional classifications: an *a posteriori* random assignment of sites to groups (to represent the minimum possible CS); and taxonomic fish clusters based on a fish community cluster analysis that produced *a posteriori* groups of the most similar fish communities that represented the maximum attainable CS for the classifications.

To further examine the relative impact of different types of dispersal barriers on stream fishes in the Midwest, the analysis of the hybrid classification approach was repeated using trophic functional guilds and reproductive functional guilds instead of fish species as the taxonomic unit of interest.

Only fish from wadeable reference streams (as identified by the Kansas Biological Survey (KBS), USEPA Region VII, and the Kansas Department of Wildlife and Parks (KDWP)) were included in the study. These are generally streams that are between 1st and 3rd order, but may include 4th and 5th order streams with lower flow. Reference streams (see below for definition) were used in order to mitigate as much of the effect of humans on natural patterns in communities as possible.

Samples utilized in this study were taken by the contributing agencies from 1988 through 2001. The majority of samples were taken from 1994 through 1997. Initially, a survey was sent out to several state agencies to see what kind of stream species and habitat data were available. Based on the survey, fish were chosen as the most widely and consistently sampled taxonomic group (instead of invertebrates) over the four-state region. Through my association with the KBS and Dr. Don Huggins, data was requested and received from the Nebraska Department of Environmental Quality (NDEQ), the Missouri Department of Natural Resources (MoDNR), the USEPA Region VII, the Iowa Deparment of Natural Resources (IDNR), and the Kansas Department of Wildlife and Parks.

The sampling protocol for stream fish was based on procedures from the USEPA (Plafkin et al. 1989, Paulsen et al. 1991, and Barbour et al. 1999). Fish were quantitatively sampled using DC pulse electrofishing and additional seining in all states except Iowa, where only electrofishing was performed. The reach length sampled was 40 times the mean wetted width of the channel.

Classification strength calculation

Fish community similarity indices were used to calculate a classification strength (CS) for the various regional and non-regional classifications being tested (after Vansickle and Hughes 2000) and included: the Sørensen (richness) index (Sørensen 1948) and the Bray-Curtis (relative abundance) index (Bray and Curtis 1957). After culling the data, a master matrix of 231 sites by 142 species was loaded into PC-ORD for Windows (version 4.20, 1999, MjM software, Gleneden Beach, Oregon), and a matrix of dissimilarities (1- similarity) among each pair of sites was generated for both indices (see Table 3 for a partial similarity matrix of sites).

The Sørensen index (S.I.) is as follows:

$$S.I. = 2c/(s_1+s_2) \qquad \text{Eq. 1}$$

Where s_1 is the number of species in community 1; s_2 is the number of species in community 2; c is the number of species both communities have in common.

The Bray-Curtis index (B.C.I.) is as follows:

$$\text{B.C. I.} = \left(\frac{1}{P}\right) \frac{\Sigma \left| X_{ik} - X_{jk} \right|}{\Sigma \; (X_{\underline{ik}} + X_{\underline{jk}})} \qquad \text{Eq. 2}$$

Where X_{ik} is the number of individuals of species k at site i; X_{jk} is the number of individuals of species k at site j; P is the number of total species at both sites combined.

Pair-wise iterative comparisons were used to calculate the relative similarity of stream communities within groups vs stream communities among groups. The variables calculated for each classification scheme were: mean similarity of sites within a group (W_i); Overall weighted mean similarity of sites within groups (W); mean similarity of sites among groups (B); and classification strength (CS = W-B with values of -1 to 1). The overall weighted mean similarity of sites within groups (W) was calculated according to Van Sickle and Hughes (2000):

$$W = \Sigma_i (n_i/N) W_i \, , \qquad \text{Eq. 3}$$

where n_i is the number of sites in group i and N is the total number of sites in all groups. The classification is judged to be stronger if the within group similarity (W) is much higher than the among group similarity (B) of fish communities.

The variables above were calculated using the MRPP (Multiresponse Permutation Procedures) analysis within PC_ORD and the MRPP extension (MRPPCONV.exe). The extension is part of the newest version of the Meansim 6 software package developed by Van Sickle and Hughes (2000) and available from the EPA's Western Ecology Division website

(http://www.epa.gov/wed/pages/models/dendro/mean_similarity_analysis.htm). The output from the Meansim 6 software includes the *p*-value for the randomization test, which randomly reassigns stream sites iteratively (10,000 times) to the same number of groups as in the classification approach being tested, and a classification strength is calculated for each of those 10,000 trials. The *p*-value is equal to the proportion of random trials that attain a higher CS than that attained by the approach being evaluated. A low *p*-value ($p<0.05$) indicates that there is some sort of "class structure" in the stream communities.

The taxonomic fish clusters (representing the maximum CS attainable) were constructed based on the flexible β cluster analysis ($\beta=-0.1$) following the methods of Lance and Williams (1967), Legendre and Legendre (1983) and Belbin et al. (1992). Resulting dendrograms were pruned to equal the number of groups in the classification being tested. The performance of each of the classifications relative to their maximum attainable CS (expressed as a percent of the maximum attainable CS) could then be compared.

Functional Guild Analysis

The classification strength analysis above was repeated using fish functional feeding guilds and reproductive guilds instead of species. Trophic functional guilds as defined by the EPA's Regional Environmental Monitoring and Assessment Program (REMAP) were used in the analysis. The EPA employed the Balon (1975) approach to classify fish based on reproductive ecology (see Table 4 for definitions of trophic and reproductive guilds used here).

A subset of the 231 reference sites (62 REMAP sites from Kansas, Missouri and Nebraska) was used in the CS analysis based on functional guilds. The CS was calculated the same as for species, but functional guilds were used as the taxonomic unit. Because the functional group analysis covered a smaller area than the species analysis, the subset of 62 sites was reanalyzed using species to provide assurance that classification strength based on functional group could be compared to the species-based analysis. This was called the "species subanalysis."

Construction of the Hybrid Classifications

The hybrid ecoregion by watershed classifications were constructed in a GIS environment. The 2-digit HUCs were overlain on top of both the Bailey Province map and the Omernik level II ecoregion map. The "select by theme" subroutine in ARC view was then used to create hybrid regions combining watersheds and ecoregions, and to calculate resultant areas of the hybrid regions created. The hybrid regions are similar in scale to the smaller *a priori* regional subdivisions (e.g., level III in the Omernik scheme; 1,000 – 10,000 mi^2) that were used in this study. (see Figures 1-5)

Data culling and database manipulation

The databases were extensively reformatted and merged to create a site by species matrix as well as two site by functional group matrices. The names for fish species were recoded to be consistent across databases following the style of the Regional Environmental Monitoring and Assessment Program (REMAP) for EPA region VII. Through extensive quality checking, synonymous, outdated, or misspelled species names were identified and corrected, and new codes were assigned to the sites so they would be compatible with the software used in the analyses (see below). The final site by species matrix contained 231 reference sites by 142 species. The final sites were culled from original datasets containing over a thousand candidate sites.

The trophic functional group matrix contained 62 sites by 12 trophic functional guilds. The reproductive functional guild matrix contained 62 sites by 9 reproductive functional guilds. Redundant functional guilds were identified and removed from the database (see Table 4 for a list of functional guilds and definitions).

Data were culled to avoid drought and flood years based on the Palmer index of drought severity (Palmer 1965) so that sporadic, temporary species absences or appearances due to these conditions could be avoided. Palmer index values were taken from the National Oceanic and Atmospheric Administration's National Climatic Data Center (NCDC) website (http://www.cdc.noaa.gov/USclimate/).

Mild to severe drought (Palmer values of –1.0 to –6.0) was found to cover most of the study area in 1989, 2000 and 2002. Therefore, those data-years were generally excluded from the study. 1993 data were excluded due to widespread flooding throughout the study area. Rarely, data from the above years were included if the stream site in question was not sampled during any other year.

The original data set contained sites that were sampled multiple times per year and over multiple years. Because of this, these data were further culled to only include one sample per site so temporal variation at a site would not interfere as much with the detection of spatial variation. In a GIS environment (ESRI's ArcView 3.3 software), sites that were 5 miles apart or closer on a stream reach and were not separated by a confluence point were judged to be from the same site, and the data from one of the sites was omitted so as not to skew the classification strength analysis. Individual fish records were deleted from any stream sample that were not confirmed identifications of a species (i.e., they had a "?" next to the record), or if the fish were hybrids, as long as the unidentified or hybrid individuals made up 5% or less of the total individuals in a community. If unidentified fish species made up more than 5% of a community, the entire stream record was deleted from the analysis. This happened only with some sites in the KDWP dataset.

These data were brought into a geographic information system (GIS – ESRI's ArcView 3.3 software) and projected onto maps (coverages or themes) depicting the various regional classifications being tested in order to assign sampling points to correct regions and envision the spatial spread of the sites. Coverages of the different regional classifications were obtained from Tina Haker at the USDA-Forest Service (HUCs based on Seaber et al. 1987, and the aquatic ecological units of Maxwell et al. 1995), from the US Forest Service website (Bailey's ecoregions - http://www.fs.fed.us/institute/ecolink.html) and from the USEPA's Western Ecology Division Website (Omernik's ecoregions - http://www.epa.gov/wed/models/ecoregions.htm – 2004). The polygon (region) and point (site) coverages were reprojected to the Albers equal area projection (reference latitude of 37.5 degrees) to look at spatial overlap between the frameworks and to create hybrid regions (Fig.s 4 and 5).

Results

Rankings of the hybrid ecoregion/HUC stream classification approaches relative to unaltered approaches

The Bailey and Omernik ecoregion frameworks were both stratified by HUC, or watersheds, to create two new hybrid ecoregion/watershed frameworks for this study. The ability of these hybrid frameworks to partition regionally different stream fish assemblages (i.e., their classification strength – CS) was compared to existing stream classification schemes to evaluate the relative influence of physical vs ecological boundaries to fish dispersal on patterns in stream fish communities in Kansas, Missouri, Iowa and Nebraska. These hybrid frameworks were also constructed to examine whether they could improve the ability of current stream classification approaches to account for spatial variation in stream ecosystems on a regional basis, which would assist in conservation, management and research goals.

Quantitative results from the stream classification strength (CS) analysis of the hybrid regions combining ecoregions and watersheds can be compared to results from unaltered classification schemes in Table 1. Both hybrid ecoregion/HUC classification approaches performed better (i.e., had a higher classification strength) than a random reassignment of stream sites to groups based on the permutation tests (p<<0.000001), no matter whether the Bray-Curtis index (B.C.I.) or the Sørensen index (S.I.) was used. Taxonomic fish cluster analyses were used to estimate the maximum attainable CS for the classification approaches in order to calibrate their CS values. Both the Bailey and Omernik hybrid ecoregion/HUC frameworks had similar maximum attainable CS values, which were 22.3% and 22.8% respectively based on the S.I., and 16.6% and 16.5% respectively based on the B.C.I. (see Table A in the Appendix).

Rankings of the classification schemes based on the ratio of their classification strength compared to the CS from the cluster analyses – in other words, the percent of the maximum attainable CS a classification approach obtained - are displayed in Table 5. From Table 5, it is clear that the hybrid ecoregion/HUC frameworks did not perform as well as the unaltered Bailey section or Omernik level III ecological regions using either the Sorensen or Bray-Curtis similarity indices. Further, hybrid regional frameworks did not perform better than the HUC framework based on the Sorensen index, but they did perform better than the HUC framework based on the Bray-Curtis index. Compared to the other stream classification approaches contained in Table 5, the hybrid regional frameworks performed better than or equal to the Maxwell et al. approach, the small geographic clusters and the Strahler stream orders based on the Bray-Curtis analysis. In the Sorensen analysis, however, the hybrid frameworks performed the worst of all regional classification approaches. Table 5 also contains CS rankings of the hybrid regions based on the functional guild analysis, which will be described below.

Performance of classification approaches based on communities defined by functional guilds

To further examine the relative influence of different types of dispersal limitations on regional patterns in fish communities, the CS analysis of the hybrid regions was done on communities based on both reproductive and trophic functional guilds (see Table 4 for a list of functional guilds used in this analysis). Both the Bailey and the Omernik hybrid ecoregion/HUC classification approaches performed better (i.e., had a higher classification strength) than a random reassignment of sites to groups based on the permutation tests, no matter whether the trophic or reproductive functional guilds were used ($p<<0.05$). However, lower p-values were produced from the permutation tests of the trophic guilds (*p*<0.0003) than the tests of the reproductive guilds (*p*<0.006).

Note in Tables 5 and 6 that patterns in relative abundance of fish reproductive guilds are not as well explained by the Omernik/HUC hybrid approach as patterns in trophic group relative abundance (B.C.I. % of the maximum CS=13% for reproductive guilds and 21% for trophic guilds). The opposite occurred when using presence/absence of guilds to compare community similarity (S.I. % of the maximum CS=40% for reproductive guilds and 34% for trophic guilds).

For the Bailey/HUC hybrid classification approach, the % of the maximum CS was higher for both indices when using trophic guilds (S.I.=38%, B.C.I=29%) than reproductive guilds (S.I.=35%, B.CI.=15%). It is also notable that the the Bailey/HUC hybrid classification produced higher % of the maximum CS values than the Omernik/HUC hybrid classification when trophic-guild communities were compared for both indices (see Table 6). Alternatively, when communities based on reproductive guild were compared, the Omernik/HUC approach outperformed the Bailey/HUC approach based on the S.I., but performed similarly based on the B.C.I. The species analysis using this same subset of sites used in the functional guild analyses (the “species subanalysis”) produced a higher % of the maximum CS for both the Sorensen and Bray-Curtis analyses than the functional guilds (% of the maximum CS = 55% and 28% respectively) (see Table 7).

Finally, in a contradictory trend to the species analyses, the analyses using functional guilds to define communities almost always revealed a higher maximum attainable CS (the CS calculated from the taxonomic clusters) when fish guild relative abundance data were used (in the Bray-Curtis analysis) than when presence/absence data were used (in the Sorensen analysis) (see Table A in the appendix).

The average classification strength of the ecoregion divided by multiple watersheds compared to the wateshed divided by multiple ecoregions

The analysis of the relative impact of physical versus ecological fish dispersal boundaries on community structure was taken to a finer level by evaluating specific areas within the hybrid frameworks where portions of multiple ecoregions are housed within a single watershed, and, vice versa, where portions of multiple watersheds are housed within a single ecoregion. Table 8 contains the average % of the maximum CS values for the species and functional guild analyses of these areas. Tables 9A and 9B contain the individual results used to calculate those averages.

The most noticeable result revealed by the average values in Table 8 is that the CS values based on functional guilds are much lower than CS values based on species (% of the maximum CS values range from 3 to 46% for functional guilds and from 46 to 83% for species). It is also obvious from the full species analysis (the analysis based on the original site by species matrix of 231 sites) that patterns in fish species communities are classified better by watershed divisions within an ecoregion than they are by ecoregion divisions that are within a watershed, no matter whether the Bailey/HUC or Omernik/HUC hybrid regions are being used. Additional species analyses (the species subanalyses) using the same subset of sites that were used in the functional group analyses (smaller n) were done to confirm this observation, and the analyses showed a consistent superior performance by the watershed divisions within an ecoregion (% of the maximum CS = 76% for the Sorensen analysis and 49% for the Bray-Curtis analysis). These are very high values compared to most of the other averages in Table 8.

Table 8 also shows that, overall, the fish communities based on trophic functional groups corresponded better with all regional divisions that were tested here than the communities based on reproductive functional groups. The exception to this was the slightly higher CS produced by the reproductive functional groups based on presence/absence data within the ecoregion divided by watersheds analysis (% of the maximum CS=42% for the reproductive groups vs 39% for the trophic groups). All other CS values calculated for the reproductive guild analysis included at least one permutation test that was not significant ($p>0.05$). This means that most the other regional divisions tested using the reproductive guilds did not perform better than a random assignment of sites to groups.

The extent of correspondence between communities based on trophic functional groups and the two major types of regional divisions in this analysis seemed to depend on whether the presence/absence or relative abundance data were used. The trophic functional groups corresponded only slightly better with watershed boundaries within an ecoregion than with ecoregion boundaries within a watershed when the presence/absence data were used (Sorensen analysis). However, when relative abundance data were used in the Bray-Curtis analysis, the watershed divided by ecoregions produced the highest average % of the maximum CS of any of the analyses using trophic functional groups. Generally, the trend is for the Sorensen analysis to yield a higher % of the maximum CS than the Bray Curtis analysis.

Results from specific regions where the ecoregion and watershed are nested within each other

An examination of specific areas where an ecoregion intersects multiple watersheds or vice versa will elucidate patterns in fish communities over a smaller area, and will help us to understand where a general trend or rule identified in the above analyses may or may not apply to all geographic areas at a finer scale. Tables 9A and 9B display the % of the maximum CS results for specific portions of the study area where an ecoregion intersects multiple watersheds and vice versa. Results from analyses of selected regions will be detailed below.

Adjacent ecoregions in the same watershed compared to adjacent watersheds in the same ecoregion

Within the Bailey/Huc hybrid regions (see Figure 4), an initial classification strength (CS) analysis was done on two ecoregions within a single watershed. The Arkansas White Red (AWR) HUC divided by the Great Plains Steppe (GPS) and Prairie Parkland (PP) Provinces showed a markedly closer correspondence with patterns in fish communities based on trophic guilds than with patterns in fish communities based on reproductive guilds (% of the maximum CS>27% for the trophic-guild communities and <4% for the reproductive-guild communities).

That section of the GPS province that is contained within the AWR watershed was then compared to the section of the GPS province contained within the Missouri watershed - an analysis of two watersheds within an ecoregion (see Table 9A and see Figure 4 for a map**).**

The relative abundances of the trophic functional groups corresponded better (B-C % of the maximum CS=46%) with these regional divisions than did the presence/absence data (the Sorensen analysis did not perform better than a random reassignment of sites to groups, $p>0.05$). Using reproductive functional groups, these regional divisions corresponded better with patterns in fish communities based on presence/absence data than relative abundance data (the relative abundance analysis did not perform better than a random reassignment of sites to groups, $p>0.05$). Also, the Sorensen analysis using reproductive groups performed better (% of the maximum CS=53%) than the Sorensen analysis using trophic groups, which did not perform better than a random reassignment of sites to groups ($p>.05$). Finally, the functional group analyses resulted in much lower CS values than the outcomes from the species subanalysis of the GPS province divided by the AWR and Missouri watersheds (species subanalysis: % of the maximum CS = 100% for the Sorensen analysis and 68% for the Bray-Curtis analysis).

Overall, the trophic groups corresponded better with the Bailey ecoregion divisions (PP and GPS) within the AWR watershed than they did with the watershed divisions (AWR and Mo) within the GPS ecoregion. However, the reproductive groups corresponded better with the watershed divisions within the GPS ecoregion than they did with the ecoregion divisions within the AWR watershed. These results support the trends identified from the table of average results (Table 8). It should also be noted that some of the regional divisions being tested here did not perform better than a random assignment of sites to groups based on the permutation tests ($p>0.05$) when functional fish guilds were used in the analysis (the non-significant values are denoted with an asterisk in Table 9A). This did not occur in the species analysis.

Comparisons of two frameworks covering the same area

Bailey vs. Omernik Ecoregions where they both intersect the Missouri and AWR watersheds

Within the two hybrid stream classfication frameworks, Bailey's GPS province intersecting Missouri and AWR watersheds, and Omernik's 9.4 ecoregion intersecting these same watersheds circumscribe overlapping but different-sized areas where an ecoregion crosses two watersheds in western Kansas and Nebraska (See Figures 4 and 5 for maps). It is informative to compare results from these two frameworks that divide the same area differently.

The results from the Bailey analysis were detailed above. Omernik ecoregion 9.4 divided by the Missouri and AWR watersheds did not correspond with patterns in trophic fish functional groups as well as with patterns in species based on both the Sorensen and Bray-Curtis analyses (trophic functional group % of the maximum CS for Sor and BC = 28% and 21%; species % of the maximum CS for Sor and BC = 52% and 30%) (Table 9A).

Based upon patterns in fish trophic functional groups, the Bailey Great Plains Steppe (GPS) Province divided by the Missouri and AWR watersheds produced a higher % of the maximum CS for the B-C analysis (CS=46%) than the Omernik ecoregion 9.4 divided by the Missouri and AWR watersheds (CS=21%). However, the Sorensen analysis came out with a non-significant CS value for the Bailey/HUC analysis (p=0.06), and a significant but low CS value for the Omernik/HUC analysis (% of the maximum CS=28%).

Four Bailey ecoregions vs. four Omernik ecoregions where they intersect the Missouri watershed

When the Missouri 2-digit HUC was divided into 4 Omernik ecoregions (8.4,9.2,9.3,9.4), these geographic divisions corresponded with patterns in trophic groups much better than with patterns in reproductive groups no matter which similarity index was used (trophic analysis: Sor % of the maximum CS=41%, B-C % of the maximum CS= 17%; reproductive analysis: Sor % of the maximum CS=28%, B-C % of the maximum CS= 8%). This same analysis performed with species instead of functional groups revealed species distributions corresponded only slightly better than trophic functional groups with the four Omernik ecoregions within the Missouri watershed, but much better than the reproductive groups (% of the maximum CS values for the species analysis were 48% for the Sorensen analysis and 25% for the Bray-Curtis analysis) (See Table 9A).

A similar analysis done on the Bailey Great Plains Palouse (GPP), GPS, PP, and Eastern Broadleaf Forest (EBF) provinces within the Missouri watershed revealed a similar level of correspondence between the presence/absence of trophic functional groups and geographic divisions when compared to the Omernik analysis above (Sor % of the maximum CS=37%). However, the relative abundance of trophic functional groups corresponded better with the Bailey geographic divisions than with the Omernik divisions (B-C % of the maximum CS=23% for the Bailey framework) (See Table 9A).

Overall Classification Strength Rankings from the analysis of specific areas where ecoregions and watersheds nest within each other

The analyses from Tables 9A, 9B and 9C were ranked (ranking not shown) to see which specific analyses and which nested regional divisions produced the highest classification strength (CS) values. Rankings of the classification strengths came out slightly differently depending on whether presence/absence data or abundance fish data were used. For the Sorensen analysis, the highest CS values were produced when similarity was calculated based on species. The Omernik 8.1 and 9.2 ecoregions in non-adjacent watersheds (Mississippi and AWR watersheds respectively) (from Table 9C), the Omernik ecoregion 9.2 divided by the AWR, Mississippi & Mo. watersheds and the subanalysis of the Bailey GPSP ecoregion divided by Mo and AWR watersheds (from Table 9B) produced the top CS values (% of the maximum CS=100% for all three nested regional divisions) (see highlighted cells in Tables 9B and 9C). This 100% value indicates that the diversity that was <u>detectable</u> among the communities was partitioned perfectly. Following closely behind these regional divisions was the Mississippi watershed divided by Omernik ecoregions 9.2 and 8.1 (the only case in which the watershed divided by ecoregions produced a high CS value for the Sorensen analysis - % of the maximum CS= 91%). The lowest CS values were produced when functional groups were used to calculate community similarity. The lowest CS value belonged to the reproductive guild analysis of the AWR watershed divided by Bailey GPSP and PP ecoregions (% of the maximum CS=3%) and the trophic guild analysis of the Bailey PP ecoregion divided by Mo and AWR Watersheds (% of the maximum CS=13%).

For the Bray-Curtis analysis, the trophic analysis of the AWR watershed divided by Bailey PP and GPS provinces performed the best (% of the maximum CS=100%), but had a low Sorensen CS (% of the maximum CS=27%) (see Table 9A). The superior correspondence of the trophic fish guilds with these specific hybrid regions will be discussed below. Other than the above-mentioned marked difference in the rankings, the same regional divisions that produced the highest CS values for the Sorensen analysis had the next-highest CS values for the Bray-Curtis analysis (see the three top-performing regional divisions highlighted in Tables 9A, 9B and 9C). However, the Bray-Curtis CS values for these other top-performing regional divisions were generally lower than their Sorensen CS values (between 58% and 68% instead of 100%), except in the case of the Omernik 8.1 and 9.2 ecoregions in non-adjacent Mississippi and AWR watersheds (% of the maximum CS=97%). Overall, the analysis showed that these sections of two different Omernik ecoregions located in non-adjacent watersheds partitioned diversity in fish communities most successfully (i.e., the divisions produced the highest CS values based on both the Bray-Curtis and Sorensen analyses) (Sor % of the maximum CS=100%; B-C % of the maximum CS=97%).

A closer look at the combined effect of being located in different watersheds and different ecoregions on stream fish communities

Using species data, a classification strength analysis was done to compare areas where two different ecoregions (Omernik 9.2 and 8.1) share the same watershed (upper Mississippi), and where they are located within two different watersheds (AWR and upper Mississippi respectively) – see Figure 5. This was done to compare the combined effect on streams of being both located in different ecoregions as well as in different watersheds to the effect of just being located in different ecoregions. The results in Table 10 indicated that there was a small gain in the % of the maximum CS based on presence/absence data if the two ecoregions were located in different watersheds (% of the maximum CS=91% for different ecoregions in the same watershed, CS=100% for different ecoregions in different watersheds). However, the larger difference was seen when relative abundance data was used (% of the maximum CS= 58% for different ecoregions in the same watershed, CS = 97% for the different ecoregions in different watersheds).

In order to evaluate whether the strong stream classifying ability of the different ecoregions located in different watersheds was due more to spatial segregation or to environmental factors associated with watershed or ecoregion boundaries, a further species analysis was done in which two sections of the same ecoregion (Omernik ecoregion 9.2) were compared where they are separated by a watershed. In short, the section of ecoregion 9.2 that is located in the AWR watershed was compared to the section of the same ecoregion that is located within the upper Mississippi watershed (the comparison still incorporates the spatial distance in the other analysis, but the ecoregion is held constant). Table 10 shows the results of this analysis along with the other two analyses described in the preceeding paragraph. The % of the maximum CS values based on the Sorensen and Bray-Curtis analyses were both 100% – higher CS values than for the other two regional analyses. The relative impact of spatial segregation was examined by comparing the analysis above to an analysis of Omernik ecoregion 9.2 divided by two adjacent watersheds (the spatial segregation was removed, but the ecoregion stayed the same, and the analysis still compared two different watersheds – AWR and Missouri). The % of the maximum CS values dropped severely compared to other values in Table 10 (Sor CS=67%; B-C CS=56%).

Discussion

Rankings of the hybrid ecoregion/HUC stream classification approaches relative to unaltered approaches

As with other regional and non-regional frameworks analyzed in Chapter One, both the Bailey and Omernik ecoregion/HUC hybrid classification approaches produced higher classification strength (CS) values than a random reassignment of sites to groups ($p<<0.000001$), indicating that both approaches had some value in classifying stream fish species communities in this part of the Midwest (Kansas, Missouri, Nebraska and Iowa). This also means that the hybrid frameworks incorporate at least some environmental criteria that are related to stream community patterns in the Midwest.

As in Chapter One, the taxonomic fish clusters based on the data used in the hybrid analyses produced a low maximum attainable CS (22.8%). This indicates a low amount of detectable variation among stream fish communities inherent to this part of the Midwest at the scale analyzed here, and with the community similarity indices employed here.

A major aim of this study was to see if the combination of two top-performing classification frameworks (the ecoregion and the watershed) into two hybrid classification approaches would correspond more closely with regional patterns in stream biota (fish) than other regional classification approaches. In contrast to this expectation, the unaltered Bailey and Omernik ecoregion frameworks both produced higher CS values than either of the hybrid ecoregion/HUC classification schemes created for this study - across both community indices (see Tables 1 and 5). However, the hybrid approaches did outperform the HUC or watershed classification approach based on relative abundance data (the Bray-Curtis index - B.C.I.), but not based on presence/absence data (the Sorensen index - S.I.). It can be concluded that this hybrid approach did not improve the ecoregions' ability to classify streams, but seems to have been somewhat successful in improving the ability of the HUCs to classify stream systems – specifically in regard to patterns in relative abundance among fish communities. It seems that the environmental factors incorporated in both ecoregion approaches aided the HUC framework in accounting for variation in stream communities. In Oregon, Van Sickle and Hughes (2000) assessed the Classification Strength of a hybrid watershed/ecoregion classification for streams by dividing the Williamette Basin HUC or watershed by Omernik level III ecoregions. In contrast to the results from this study, their analysis, based on patterns in fish community similarity, suggested that this hybrid classification may be stronger than either the ecoregion or HAU alone when applied to streams. However, I believe this stronger performance of their hybrid classification may have been due to the hybrid classification's finer scale than the other frameworks it was being compared to.

Given the generally poor to similar performance of the hybrid classification approaches relative to the unaltered regional stream classification approaches, this study does not support their general use at the scale of this analysis in this part of the Midwest.

Another major question addressed with this research was the relative importance of physical barriers to dispersal compared to ecological barriers to dispersal on stream fish communities in Kansas, Nebraska, Iowa and Missouri. Since the addition of ecoregion boundaries improved the CS of the HUC framework (according to the B.C.I.), but the addition of HUC boundaries did not improve the Bailey or Omernik ecoregion frameworks, this can be taken as the first piece of evidence that ecological boundaries to dispersal are more influential to fish community structure than physical boundaries to dispersal in this part of the country. This conclusion is somewhat expected, because this part of the Midwest has little topographic variation. This conclusion is in agreement with Cross et al. (in Hocutt and Wiley 1986), who studied the western Mississippi basin, and noted that most fish species occupied parts of different drainage basins, and no one species was present throughout a single river drainage.. Alternatively, this conclusion is in contrast to the findings of Mcormick et al. (2000), who showed that catchments corresponded more closely with patterns in fish community diversity than ecoregions in the Mid-Atlantic Highlands. It should be noted that the improvement of the classification strength of the HUC classification approach for streams was not large (between 2% and 3% - see Table 1), and was only applicable to patterns in relative abundance, not richness. Additional evidence revealing the relative influence of ecological versus physical boundaries to dispersal on fish communities, which was gleaned from an examination of specific subregions within the study area, will be discussed below.

Performance of classification approaches based on communities defined by functional guilds

The use of trophic and reproductive functional guilds to define communities enabled the study to evaluate the ability of the hybrid ecoregion/HUC frameworks to predict patterns in fish communities based on their ecological requirements (see Table 4 for functional group definitions) in three states within the study area (Kansas, Nebraska and Missouri). The functional guild analysis also allowed a more detailed examination of the kinds of landscape-scale influences that have the strongest impacts on fish communities (i.e., the relative influence of watersheds versus ecoregions).

Both hybrid classification approaches performed better than a random reassignment of sites to groups based on the permutation tests ($p<0.006$), which indicates that they had some value in classifying regional patterns in trophic and reproductive fish guilds. This suggests that both hybrid classifications incorporated environmental criteria that were at least somewhat related to patterns in stream fish functional guilds in this part of the Midwest.

The communities defined by trophic guilds generally corresponded more closely (i.e., had a higher % of the maximum CS) with both the Bailey and Omernik hybrid ecoregion/HUC frameworks than the communities defined by reproductive guilds. However, in the one exception to this trend, the reproductive guilds corresponded to the Omernik/HUC hybrid framework's regional divisions better than the trophic guilds when presence/absence data was used (S.I.) (see Tables 5 and 6).

Since the trophic guilds generally produced a higher % of the maximum CS than the reproductive guilds for both classification approaches, it may be concluded that environmental factors that facilitate the presence of food (i.e., certain macroinvertebrates, plankton and smaller prey-fishes) are being accounted for more comprehensively in both hybrid frameworks than environmental factors influential to egg-laying, egg development and nesting habits.

However, the superior correspondence of richness patterns of reproductive guilds with Omernik/HUC hybrid regions may indicate that Omernik ecoregions stratified by HUC boundaries are more able to partition areas that contain distinct stream substrate types, because that is an environmental parameter very closely associated with egg laying and nesting habits in fish. It should be noted that the functional guilds that blink on and off on either side of these hybrid boundaries most likely have low populations, because the diversity in these functional guilds was not well-partitioned by the Bray-Curtis index based on relative abundance.

The fact that patterns in relative abundance of trophic guilds corresponded with both hybrid frameworks better than patterns in reproductive guilds indicates that the hybrid regions are more predictive of the success of functional feeding guilds – patterns in the realized trophic niches of fish. Due to the closer correspondence between trophic communities and the Bailey/HUC classification approach based on presence/absence data, it can also be suggested that the Bailey/HUC approach is more predictive of patterns in the potential trophic niches of fish than the omernik/HUC framework. The results also indicate that the Omernik/HUC framework is more predictive than the Bailey/HUC framework of patterns in the potential reproductive niches of fish, but not the success of fish within those reproductive niches.

An exploration of the poor correspondence between functional guilds and hybrid frameworks compared to species

Cluster analysis helps to reveal spatial clumping in types of functional guild communities

It is notable that both types of functional guilds corresponded poorly with the hybrid regional divisions (i.e., had lower % of the maximum CS values) compared to the correspondence of patterns in species with these regional divisions (see Table 6). Poor correspondence of ecoregion boundaries with stream macroinvertebrate functional feeding groups compared to species was also found by Harding et al. (1997) in New Zealand. In addition, Poff and Allan (1995) found comparatively poor correspondence between fish stream communities defined by a variety of functional attributes (including trophic habits) and Omernik's Level III ecoregion boundaries in Wisconsin and Minnesota.

This result could be due to the fact that functional groups are very similar within and across regional subdivisions, and that stream functional group composition is very homogeneous across the study area. This homogeneity would be indicated by very low CS values for the hybrid regions based on functional groups. A look at Table 7 confirms this possibility, with the raw CS values for the functional guilds reaching a high of 6.9%. To confirm whether or not stream functional group composition across the study area was indeed homogeneous, the taxonomic similarity clusters used to calculate the maximum classification strength values were projected onto a map in a GIS to see if streams from the same cluster clumped together spatially. When the cluster dendrogram was pruned to 5 or 6 taxonomic clusters (the same number of groups that were compared in the hybrid frameworks), they did not clump together spatially (maps not shown).

Three types of reproductive guild communities show geographic affinities

A further inspection of the cluster dendrogram based on the Sorensen Index revealed that there were three distinct taxonomic clusters formed by both the reproductive guild and trophic guild communities. Therefore, the three S.I. clusters from both of the functional guild analyses were projected onto a map (see Fig.s 6 and 7) to reveal whether spatial clumping would occur within these larger clusters. The reproductive guild clusters produced distinct geographic clumping (see the encircled areas in Fig. 6), but these regional clusters did not correspond to any of the regional classification approaches tested here at any scale. Cluster one stream communities were diffusely spread throughout the whole study region, but were almost the exclusive type of functional guild community (barring two exceptions) inhabiting an area from eastern Kansas into central Missouri (see corresponding circled area in Figure 6). Streams from cluster one contained representatives from the most reproductive guilds compared to the other two clusters. The typical stream assemblage in cluster one was characterized by the presence of four guilds that occupied at least 70% of the streams in the cluster according to ranked stream occupancy data (Table 11). These most common guilds were: nest-guarders on sand or gravel (Lithob2), non-guarders of eggs broadcast on plants (Phyto a1), nest-associated fish (Nestasso) and non-guarders that spawn on open substrate (LythoA1), in the order of % of streams occupied (see Table 4 for a list of codes and definitions for functional guilds). Collectively, streams from cluster one contained species from almost all of the reproductive guilds except the phyto-b2 guild, which is composed of fish that guard a nest of eggs laid in plant material. The phyto-b2 guild was the only guild not found within any streams assessed in this study. Cluster one also was the only cluster to contain streams with fish that guard eggs attached to plants (Phytob1).

The other two clusters of reproductive guild communities were localized over a more specific geographic area than cluster one, although both contained streams that were geographic outliers. Cluster two ranged from a small area in northwest Kansas through most of Nebraska - with the exception of Nebraska's southeast corner (i.e., the range was the northwest part of the study area). Streams in cluster two contained representatives from the fewest guilds of any of the clusters (five guilds out of nine), meaning they had low guild-diversity. According to the ranked stream occupancy data (Table 11), a typical stream in cluster two contained the following guilds: nest-guarders on sand or gravel (Lithob2), non-guarders that spawn on open substrate (Lithoa1), guarders of eggs attached to rocks (Lithob1) and non-guarders that bury their eggs in the substrate (Lithoa2), in the order of % of streams occupied.

Cluster six (the third cluster) was mostly located in central Kansas, but ranged northward into southeast and east-central Nebraska (See Figure 6). According to the ranked stream occupancy data (Table 11), a typical stream in cluster six contained the following guilds: guarders of eggs attached to rocks (Lithob1), nest-guarders on sand or gravel (Lithob2), nest-associated fish (nestasso), and non-guarders that spawn on open substrate (LythoA1), in the order of % of streams occupied. Cluster six also contained the most streams occupied by live-bearing fish; only one stream with live bearing fish was found outside of cluster six.

Three types of trophic guild communities do not show strong geographicaffinities

Of the three trophic guild clusters, only cluster six clumped geographically (see Fig. 7). Cluster six was located mainly throughout Kansas, but spread up into southeast Nebraska. According to rank occupancy data (Table 12), the typical stream in cluster six contained: benthic insectivores (Bins), benthic macrophagic omnivores (Bmacomni), fish that were both invertivores and piscivores (Invpisc) and invertivores (inv), in order of % of streams occupied. The streams from the other two clusters (clusters one and three) were diffusely spread throughout the study area (see Fig. 7). However, cluster three represented the major type of stream functional group community (with only two exceptions) that inhabited the eastern part of the study area. Collectively, cluster three stream communities had higher stream occupancy rates (above 70%) from more trophic functional guilds than the other two clusters (i.e., had a higher guild diversity per stream than the other clusters – see Table 12). The highly diverse streams in cluster three typically contained the following guilds: benthic insectivores (Bins), fish that were both invertivores and piscivores (Invpisc), non-benthic insectivores (Ins), benthic herbivores (Bherb), benthic macrophagic omnivores (Bmacomni), non-benthic macrophagic omnivores (Macomni) and non-benthic invertivores (Inv), in order of % of streams occupied.

Types of functional guild communities show regional affiliations that could be predicted by regional classification frameworks at a broader scale

Since regional divisions were indeed apparent among the Sorensen taxonomic clusters of communities based on reproductive guilds, and somewhat apparent among the Sorensen clusters of trophic guild communities, it can be concluded that the distribution of guild communities is not highly homogeneous over the Kansas, Missouri and Nebraska study area. This is the opposite of the homogeneity indicated by the low CS values from the hybrid classification approach. This result indicates that a regional framework could potentially account for patterns in fish reproductive guild communities. However, the examination of clustering patterns of ecological guilds indicates that the hybrid regions are not incorporating major limiting ecological influences to streams into their design, or are not circumscribing the correct scale to delineate those patterns. This is especially true for reproductive guilds.

Upon further examination of the scale at which spatial clumping of stream guild communities was revealed in Figures 6 and 7, it seems that processes at the intermediate scale (the scale of the hybrid regions) do not have strong control over the guild-composition of communities, but that processes at a broader regional scale (e.g., the scale of Omernik's level II ecoregions – see Table 2) may be controlling guild distribution patterns, because there is distinct geographic clumping at that broader scale. Again, this is especially true for the reproductive guilds (see Figure 6).

The trophic guilds did not reveal as much influence from broader-scale regional processes, because spatial clumping was only apparent in one of the three large trophic guild clusters (Figure 7). The diffuse, random spread of clusters one and three indicate that, in contrast to reproductive guilds, local processes may have more control over the distribution of trophic guilds that make up these communities.

Finally, it must be stressed that the discussion above is based on the analysis of distributions of guilds (their presence or absence in a certain location), not on the analysis of their relative abundance, or success, in a certain location. As mentioned above, the clusters of similar guild communities based on relative abundance data did not reveal distinct geographic clumping at any scale (i.e., clusters of guild communities based on the success of certain guilds were spread more homogeneously throughout the study area). This result indicates that the success of both reproductive and trophic guilds may be more dependent on local processes (e.g., the amount of local physical disturbance leading to localized siltation and habitat homogenization), than intermediate or broader-scale processes (e.g., climate and major landcover impacts), which are incorporated into the hybrid stream classification scheme and other regional stream classification approaches.

It should be noted that this is the first multi-state cluster analysis of patterns in stream fish communities based on functional guild for this part of the United States.

Distinct shifts in types of reproductive guild communities from the Southeast to the Northwest are identified

Another way to interpret the geographic spread of the reproductive guild community clusters in Figure 6 is that there is a distinct gradient in guild community types, and therefore types of streams, as one moves from the southeast to the northwest within the study area. It is apparent in the clusters of reproductive guild communities that, as we move from the southeast to the northwest, the stream communities are mostly of the type from cluster one initially. Then, in the central part of the study area, streams from cluster six mostly take over but are blended with streams from cluster one. Finally, in the northwest portion of the study area, the streams are a mix of cluster one types and cluster two types (regions of different guild-types are demarcated by straight lines in Figure 6).

This pattern could indicate that there is a gradient of environmental conditions that are more distinct among these three regions of guild community similarity that are controlling the distribution of potential ecological niches in streams. Perhaps, the gradient is one of changing moisture and temperature combinations. This would be logical, since there is an east to west drying trend, and a south to north cooling trend in the study area. Perhaps, the gradient in precipitation and temperature is strongly impacting in-flow of debris and erosion into the streams, thereby impacting the types of substrates that are in the stream, which are critical to the types of reproductive guilds that can occupy the stream. In support of this reasoning, Rabeni and Smale (1995) found that changes in lithophilous spawners (fish that lay eggs in sand or gravel) were most closely connected with siltation in streams. Further examination of these distinct regions could help scientists and managers understand the large-scale driving forces behind these patterns in reproductive guild communities, and the stream ecosystems in which they live.

In contrast, the spatial spread of clusters of trophic guild communities seems to be much more diffuse throughout the study area. This indicates once again that there is potentially less influence of broad-scale regional environmental processes over trophic guild community composition than intermediate scale or local-scale environmental processes.

The average classification strength of the ecoregion divided by multiple watersheds compared to that of the watershed divided by multiple ecoregions reveals which framework may be more applicable at different scales

The values in Table 8 were constructed from regional CS analyses done on specific subsections of the hybrid frameworks where an ecoregion was divided by multiple watersheds or where a watershed was divided by multiple ecoregions. The average values from Table 8 were then used to make a simpler table (Table 13) to compare whether the division of an ecoregion by multiple watersheds (EW) was better at partitioning diversity among fish communities than the division of a watershed (HUC) by multiple ecoregions (WE) in this part of the country. The results may indicate whether one classification approach would work better as the coarser-scale organizing framework or the finer-scale organizing framework for a regional stream classification approach in this area. Table 13 reveals that, overall, the ecoregion divided by multiple watersheds (EW) more successfully partitioned diversity in stream fish communities than the watershed divided by multiple ecoregions, especially based on presence/absence data. The result holds for both the Bailey and Omernik hybrid frameworks.

Specifically, from Table 13, patterns in species were partitioned the best by EW based on both similarity indices. In contrast, patterns in relative abundance of trophic guilds corresponded best with a watershed that was divided by multiple ecoregions, but patterns in presence/absence of trophic guilds corresponded best with the ecoregion divided by multiple watersheds. The diversity in the presence/absence of reproductive guilds was partitioned best by the ecoregion divided by watersheds, but the analysis using relative abundance of reproductive guilds did not produce a classification strength that was better than a random assignment of sites to groups for either type of analysis (EW or WE).

With few exceptions, these results indicate that the ecoregion may be the better coarser-scale organizing framework than the watershed in a nested hierarchical approach to classifying stream ecosystems. Further, the results indicate that watersheds may be more useful than ecoregions as finer-scale subunits within the larger ecoregion for partitioning diversity in stream ecosystems in this part of North America.

These results convey a potentially major piece of evidence regarding the relationship between scale and the relative influence of ecological boundaries to fish dispersal vs physical boundaries to dispersal on fish community structure. Although this is not the only explanation for the trends noted above, the evidence suggests that environmental factors that are associated with the ecoregion (ecological limitations to dispersal) have a greater impact on fish community structure at a coarser scale, while the physical boundaries to dispersal represented in the watershed are more influential when used to make finer-scale subdivisions within the ecoregion framework. This gives support to the contention of Omernik and Bailey (1997), and the findings of Feminella (2000) that ecoregions and watersheds can be complementary rather than competing regional classification frameworks.

In the one departure from the superior performance of the ecoregion divided by watersheds, patterns in the relative abundance of trophic guilds corresponded more closely to the watershed divided by ecoregions. This could be interpreted to mean that for patterns in trophic guild relative abundance, that the watershed seems to be the most appropriate broader-scale organizing feature, and the ecoregion seems to be the finer scale organizing feature nested within the watershed. However, this conclusion may be flawed, because the average value from the source table (Table 8) for Table 13 was likely skewed by an extremely high CS outcome from an analysis of a specific region – the Arkansas White Red (AWR) watershed divided by the Bailey Great Plains Steppe (GPS) and Prairie Parkland (PP) provinces. The result from this region represents the exception to the rule that has been elucidated above, in which all of the other analyses indicated that a framework in which the ecoregions are subdivided by watersheds is more reflective of patterns in fish communities than watersheds divided by ecoregions in this part of the Midwest. Possible reasons for this unique outcome from this specific region will be discussed below.

Discussion of results from specific regions where the ecoregion and watershed are nested within each other

Adjacent ecoregions in the same watershed compared to adjacent watersheds in the same ecoregion

A discussion of specific areas where an ecoregion intersects multiple watersheds or vice versa will elucidate patterns in fish communities over a smaller area, and will help us to understand where a general trend or rule identified in the above analyses may or may not apply to all geographic areas at a finer scale (see Tables 9A, 9B and 9C for CS values from specific regions within the study area).

The success of the AWR watershed divided by the Bailey PP and GPS provinces (ecoregions) described above is worthy of further exploration, because it represents a departure from the general rule elucidated in Table 13. Diversity among communities based on relative abundance of trophic guilds was partitioned perfectly

(% of the maximum CS=100%) by these ecoregions nested within the AWR watershed, but diversity among communities based on the presence or absence of trophic guilds was poorly partitioned (% of the maximum CS=27% - see Table 9A). These results indicate that the ecoregion does a better job of partitioning diversity among trophic guilds (i.e., the ecoregion approach accounts for ecologically influential factors structuring trophic niches in streams) in this specific part of the study area. However, this conclusion does not apply to other regions assessed in this study.

To further examine the trends identified in Table 13, the section of the GPS province that is contained within the AWR watershed (one of the regions used in the above analysis) was then compared to the section of the GPS province contained within the Missouri watershed; an analysis of multiple watersheds within an ecoregion (see Table 9A and see Figure 4 for a map). The trophic groups corresponded better with the Bailey ecoregion divisions (PP and GPS) within the AWR watershed, while the reproductive groups corresponded more closely with the watershed divisions (AWR and MO) within the GPS ecoregion. This comparison provides region-specific evidence to support the trends identified in Table 13.

One other point to mention is that some of the finer-scale regional divisions that were tested here did not produce a CS that was higher than a random assignment of sites to groups based on the permutation tests when functional fish guilds were used (the non-significant values are denoted with an asterisk in Table 9A). However, this did not occur in the species analysis for any of the finer-scale region-specific assessments of CS. Perhaps, functional groups may have not been as distinct among regional divisions as species because functional group composition may not differ much among least-disturbed or reference streams from different ecoregions, although taxonomic make-up may be very different. This was found to be the case by Statzner et al. (2001) in which their functional group analysis of patterns in macroinvertebrate communities revealed that there were no great differences among reference streams located in different ecoregions, but that functional group composition did differ among reference vs perturbed European streams.

Comparisons of two frameworks covering the same area

As detailed previously in the results, the regional CS of the two ecoregion/HUC hybrid frameworks were compared where they subdivide a similar area in a spatially different way to contrast the ability of these two hybrid frameworks to partition community diversity in streams. The first comparison included the Bailey GPS province versus the Omernik level II ecoregion 9.4 where they are intersected by the Missouri and AWR watersheds (see Figures 4 and 5 for maps). This was a comparison of portions of the hybrid frameworks where the ecoregion was divided by multiple watersheds (EW). The second comparison included the Missouri watershed divided by four Bailey ecoregions (GPP, GPS, PP and EBF) versus the Missouri watershed divided by four Omernik ecoregions (8.4, 9.2, 9.3 and 9.4) (See Figures 4 and 5 for maps). This was a comparison of portions of the hybrid frameworks where the watershed was divided by multiple ecoregions (WE).

Overall, types of reproductive guild communities were partitioned very poorly by both of these hybrid frameworks (i.e., had low % of the maximum CS values) in both of the comparisons, no matter which index was used. Also in both comparisons, the species communities were partitioned better by both hybrid frameworks than either type of functional guild community. However, the most distinctive contrast in CS among the two hybrid frameworks was revealed when trophic functional guilds were used in the analysis. In both comparisons, the Bailey hybrid framework partitioned diversity in the relative abundance of trophic guild communities distinctly better than the Omernik hybrid framework covering the same area (see Table 9A). When presence/absence data was used, however, the first comparison revealed that the Omernik hybrid framework partitioned diversity in trophic guild communities more effectively than the Bailey framework, which did not produce a CS higher than a random reassignment of sites to groups. There was no difference in the performance of the two hybrid frameworks found in the second comparison based on the Sorensen (presence/absence) analysis.

The higher CS values based on the Bailey/HUC divisions in the first analysis could be due to the fact that the Bailey GPS province does not run as long laterally from east to West as the Omernik 9.4 ecoregion (See Figures 4 and 5). This wider area coverage causes the Omernik ecoregion 9.4 to encompass a wider range of precipitation and soil types, which would influence a broader range of stream flows and stream types reflected in the trophic functional groups present. This result could mean that there is a specific region of change (or sharp gradient) in functional groups present -and therefore stream type - as we move from east to west that the bailey framework is accounting for, but the Omernik framework is not (due to heavier focus on climate in the Bailey framework). Also, the Bailey GPS province is longer longitudinally where it intersects with the Missouri watershed than the Omernik 9.4 ecoregion, so the superior CS of the Bailey hybrid framework might indicate that there is less of a north to south gradient in trophic functional groups.

Overall classification strength rankings of specific areas where ecoregions and watersheds nest within each other

The analyses from Tables 9A, 9B and 9C were ranked (ranking not shown) to see which specific analyses and which nested regional divisions produced the highest classification strength (CS) values. Rankings of the classification strengths came out slightly differently depending on whether presence/absence data or abundance fish data were used. For the Sorensen analysis, the highest CS values were produced when similarity was calculated based on species (see top CS values associated with specific regions highlighted in Tables 9A, 9B and 9C), and the regional divisions generally consisted of an ecoregion subdivided by multiple watersheds. The % of the maximum CS for the three top-performing regions was 100%. However, the % of the maximum CS for both hybrid frameworks as a whole was never greater than 68% (see Table 6). Obviously, since we did not get 100% of the maximum CS for the whole hybrid frameworks, stream community diversity in these specific regions is better-partitioned by the hybrid framework than stream community diversity in the study area as a whole, and may be a good framework to apply in these specific areas (or may provide insight into techniques for finer-scale stream classification in these specific areas).

Following closely behind the top-performing regional divisions based on the Sorensen analysis was the Mississippi watershed divided by Omernik ecoregions 9.2 and 8.1 (see Table 9B and Figure 5). This species community analysis was the only case in which the watershed divided by ecoregions (WE) produced a high CS value for the Sorensen analysis (% of the maximum CS= 91%). This result indicates that the watershed and ecoregion may have different roles in this northeast part of the study area in shaping stream communities than they do in the rest of the study area. In these different roles, the watershed may be more influential to broader-scale patterns in fish species communities, but the ecoregion may be a better tool for finer delineation of ecologically different regions within the watershed.

The functional guild analyses within these specific regions were consistently ranked the lowest of all analyses, no matter which index was used, with one exception. Based on the Bray-Curtis index, the trophic analysis of the AWR watershed divided by Bailey PP and GPS provinces performed the best (% of the maximum CS=100%), but had a low Sorensen CS (% of the maximum CS=27%) (see Table 9A) (the possible reasons for this were discussed above). Otherwise, the same specific regions that produced top CS values in the Sorensen species analysis produced the next-highest CS values in the Bray-Curtis analysis. However, the Bray-Curtis CS values for these other top-performing regional divisions were generally lower than their Sorensen CS values, except in the case of the Omernik 8.1 and 9.2 ecoregions in non-adjacent Mississippi and AWR watersheds (% of the maximum CS=97%) (See Figure 5 for a map). Overall, the rankings showed that these sections of two different Omernik ecoregions located in non-adjacent watersheds partitioned diversity in fish communities most successfully (i.e., the divisions produced the highest CS values based on both the Bray-Curtis and Sorensen analyses) (Sor % of the maximum CS=100%; B-C % of the maximum CS=97%).

A closer look at the combined effect of being located in different watersheds and different ecoregions on stream fish communities:

Are these effects overshadowed by the influence of spatial proximity on stream community similarity?

Of course, the difference in stream communities in these regional divisions that were the most successful in partitioning diversity could be due to a variety of factors associated with being in different watersheds, different ecoregions, or being so far apart spatially. Therefore, an analysis using species was performed to compare the combined effect on streams of being both located in different ecoregions as well as in different watersheds to the effect of just being located in different ecoregions. For this analysis, the CS of the successful Omernik ecoregions (9.2 and 8.1) located in non-adjacent watersheds (Upper Miss. and AWR) (regional division #1) was compared to the CS of the same two ecoregions where they are adjacent to one another and share a watershed (Upper Miss.) (regional division #2) (see Table 10 and Figure 5).

Both the Bray-Curtis and Sorensen CS results in Table 10 revealed a greater ability to partition diversity in fish communities if two different ecoregions were located in different watersheds than if they were located in the same watershed (i.e., regional division #1 had a higher CS than regional division #2). The larger gain in ability to partition diversity was seen when relative abundance data was used in the analysis rather than presence/absence data (a 39% increase in the % of the maximum CS using relative abundance versus a 9% increase in CS using presence/absence data).

Uncertainty in what to conclude from the above comparison is introduced when we realize that the comparison between #1 and #2 incorporates variability in spatial proximity in addition to variability in whether streams are sharing a watershed or are in different watersheds. In order to evaluate whether the stronger stream classifying ability of the different ecoregions located in different watersheds (regional division #1) was due more to spatial segregation or to environmental factors associated with watershed boundaries, a further species CS analysis was done in which two sections of the same ecoregion (Omernik ecoregion 9.2) were compared where they are separated by a watershed. In short, a section of ecoregion 9.2 that is located in the AWR watershed was compared to the section of the same ecoregion that is located within the upper Mississippi watershed (the comparison still incorporates the spatial distance in the other analysis, but the ecoregion is held constant – regional division #3). The % of the maximum CS values based on the Sorensen and Bray-Curtis analyses were both 100% for this new regional analysis – generally higher CS values than for the other two regional analyses (#'s 1 and 2 – see Table 10). The performance of these three regional divisions shows that varying the ecoregion or varying the watershed in which streams were located did not produce an associated increase in variability (i.e., a high CS) in stream communities among those regional divisions. However, in the analyses in which spatial distance between the groups of streams was varied, the adjacent regions showed less variability among their stream communities (their CS decreased) relative to those stream communities in spatially segregated regions.

The relative impact of spatial segregation was further examined by comparing the analysis of #3 to an analysis (#4) of Omernik ecoregion 9.2 divided by two adjacent watersheds (the spatial segregation was removed, but the ecoregion stayed the same, and the analysis still compared two different watersheds – AWR and Missouri). For the analysis of #4, the % of the maximum CS values dropped severely (at least a 33% decrease) compared to the CS values for analysis #3 (see Table 10).

Therefore, there seems to be consistent evidence from the set of analyses described above that spatial distance between two streams is much more likely to produce distinctly different stream communities than the location of those streams in different ecoregions or different watersheds. In essence, physical boundaries to dispersal (watersheds) and ecological boundaries to dispersal (ecoregions) in the area of the above assessments do not seem to influence the distribution and structure of stream fish species communities as strongly as spatial separation between communities. Perhaps, spatial separation of stream communities was found to be important because it has had an important historic influence on speciation. In the absence of extreme topographic boundaries to dispersal in this area, spatial distance may be the most important barrier operating to prevent populations from interbreeding, and thereby contributing to allopatric speciation. Also, the dewatering of many streams in the region may add to the influence of spatial separation by decreasing the connectedness of stream systems as well as the total amount of aquatic habitat available over the landscape. Spatial separation could also be a surrogate for as-yet-undetected differences in environmental conditions that are influential to streams and their fish communities at the scale of this analysis. This finding that spatial separation is most closely associated with differences in stream fish communities is corroborated in the first chapter in which the regional framework based on geographic proximity generally produced the highest CS values.

Conclusions

Overall performance of the hybrid ecoregion/watershed approach

The hybrid Bailey and Omernik ecoregion by watershed classification approaches analyzed with this study did not represent an improvement over the classification strength of either of the unaltered ecoregion approaches in the study area (Kansas, Missouri, Nebraska and Iowa). However, the two hybrid approaches did represent a small improvement over the ability of the unaltered 4-digit HUC approach to classify streams based on relative abundance of fish species (Bray-Curtis index – B.C.I.).

Given the generally poor to similar performance of the hybrid classification approaches relative to the unaltered regional stream classification approaches, this study does not support their use at the scale of this analysis in this part of the Midwest. However, given that this was the first time hybrid regions were constructed and tested on streams for this part of the Midwest, further testing of the hybrid regions, and construction of these regions at different scales, would be prudent to assess whether they can be applied as a structuring framework to conduct research, conservation, management and monitoring of streams.

Relative influence of physical versus ecological boundaries to dispersal

An analysis of the ability of these hybrid frameworks to classify species richness and relative abundance can also inform us as to the relative influence of ecological boundaries to fish dispersal (represented by the ecoregion) versus physical boundaries to dispersal (represented by the watershed), and how those two influential boundaries on organismal distribution and survival interact differently in different geographic areas.

Since the addition of the HUC boundaries improved the CS of the HUC framework, but did not improve the Bailey or Omernik ecoregion frameworks' classification strength, this provides some initial evidence that ecological boundaries to dispersal are more influential to fish community structure than physical boundaries to dispersal in this part of the U.S.

The CS analysis of the hybrid framework based on functional feeding guilds

Both hybrid classification approaches performed better than a random reassignment of sites to groups based on the permutation tests, which indicates that they had some value in classifying regional patterns in functional feeding and reproductive fish guilds. However, both types of functional guilds corresponded poorly with hybrid regional divisions compared to the correspondence of the hybrid divisions with patterns in species.

Surprisingly, the poor correspondence between functional groups and the hybrid regions was not due to the fact that types of functional guild communities do not show distinct geographic affinities. A cluster analysis revealed that there was distinct geographic clumping in three taxonomic clusters constructed from the reproductive guild community data. When projected onto a map, three regions of distinct combinations of reproductive guild communities were revealed, which seem to indicate a gradient of influential conditions that may run from the southeast to the northwest portion of the study area. The scale at which these geographic groups of similar guilds were identified indicates that broader-scale environmental processes (including climate cycles impacting regional temperature and precipitation gradients) than those associated with the intermediate scale of the hybrid framework analyzed here may be shaping patterns in reproductive guilds.

Since the trophic guilds generally produced a higher CS than the reproductive guilds for both hybrid approaches, it may be concluded that environmental factors that facilitate the presence of food (i.e., certain macroinvertebrates, plankton and smaller prey-fishes) are being accounted for more comprehensively in both hybrid frameworks than environmental factors influential to egg-laying, egg development and nesting habits. However, the superior correspondence of the Omernik framework with patterns in richness of reproductive guilds indicates that the Omernik framework stratified by HUC boundaries is more able to partition areas that contain distinct stream substrate types, because that is an environmental parameter very closely associated with egg laying and nesting habits in fish.

It should be noted that this is the first multi-state cluster analysis of stream fish communities based on functional guild for this part of the United States.

Region-specific analyses

An overview of the performance of portions of the study area where multiple ecoregions are nested within a watershed or, alternatively, where multiple watersheds are nested within an ecoregion indicates that environmental factors that are associated with the ecoregion (ecological limitations to dispersal) have a greater impact on fish community structure at a coarser scale, while the physical boundaries to dispersal represented in the watershed are more influential when used to make finer-scale subdivisions within the ecoregion framework. This supports the contention of

Omernik and Bailey (1997) that the watershed and ecoregion are complementary frameworks, and are best used in combination to classify streams in certain regions.

Since some of the smaller regional divisions performed much better than the overall hybrid framework (e.g., some regional subdivisions attained 100% of the maximum attainable CS), stream community diversity in these specific regions is better-partitioned by the hybrid framework than stream community diversity in the study area as a whole. This indicates that the hybrid framework may be a good framework to apply in these specific areas (or may provide insight into techniques for finer-scale stream classification in these specific areas). However, as stated above, the hybrid framework did not seem to partition diversity over the whole study area as well as the ecoregion frameworks, and therefore is not recommended for general use as a classification approach for this part of the Midwest.

Finally, an analysis of several smaller regional divisions that shared adjacent ecoregions, shared adjacent watersheds, or were spatially segregated gave evidence that physical boundaries to dispersal represented by watersheds and ecological boundaries to dispersal represented by ecoregions do not seem to influence the distribution and structure of stream fish communities as strongly as spatial separation between communities at the scale of this analysis. This finding is consistent with the superior performance of the geographic distance classification framework in Chapter one.

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TABLES AND FIGURES FOR CHAPTER TWO

Group Name	% of maximum attainable CS (S.I.)	% of maximum attainable CS (B.C.I.)
2-digit HUCS/Bailey Province Hybrid	56	50
2-digit HUCS/Omernik Level II Hybrid	68	51
Bailey Sections	75	55
4 digit HUCs	73	48
Omernik Level III Ecoregions	75	57
Maxwell River Basins	69	50
Geographic Distance Clusters	79	43
Strahler Order	30	27

Table 1. A comparison of the % of the maximum attainable Classification Strength (CS) for hybrid ecoregion/HUC regional stream classifications to unaltered regional and non-regional stream classification approaches. CS values were based on similarities among stream fish species communities.

Classification Schemes		Area (mi^2)	Defining Criteria
Watersheds (HUCs)	2-digit	10,000s - 100,000s	topography (extraction from digital elevation models (DEM's))
	4-digit	1,000s	extraction at a finer scale
Bailey Ecoregions	Provinces	10,000s	climate, soils and potential natural vegetation (focus on geoclimatic setting)
	Sections	1,000s - 10,000s	climate, geology, landform, soils, potential natural vegetation, and some land use/cover (focus on geoclimatic setting and glacial influences)
Omernik Ecoregions	Level II	10,000s - 100,000s	landform, geology, land use/cover, climate, soils, potential natural vegetation (focus on land cover, but the criteria used varies somewhat based on its importance to the region)
	Level III	1,000s - 10,000s	
Hybrid Classification: Bailey Ecoregions/Watershed (HUC 2)	Provinces / HUC	1,000s - 10,000s	ecoregion stratified by 2-digit HUC boundaries
Hybrid Classification: Omernik Ecoregions/Watershed (HUC 2)	Level II / HUC	1,000s - 10,000s	ecoregion stratified by 2-digit HUC boundaries
Maxwell et al. (Aquatic Ecological Units)	Subregions	10,000s	geology, landform, climate, biogeographic patterns for aquatic biota and watershed boundaries
	River Basins	1,000s-10,000s	
Neutral Geographic-distance Clusters	Larger Clusters	10,000s	geographic distance between sites
	Smaller Clusters	1,000s	
Strahler Stream Order	N/A	N/A	stream order identified by monitoring agency
Non-spatial Random Clusters (Minimum CS)	Larger Clusters	N/A	random assignment of sites into a comparable number of groups to other classification schemes (10000 iterations)
	Smaller Clusters	N/A	
Fish Similarity Clusters (Maximum CS)	Larger Clusters	N/A	maximum fish community similarity based on the flexible beta cluster analysis
	Smaller Clusters	N/A	

Table 2. Characteristics of stream classifications and hierarchical levels of interest to this study.

Site	Ecoreg.	KS096S	NE086S	NE094S	NE081S	NE096S	KS078S	KS097S	KS100S	NE077S	NE080S	KS081S	KS085S	KS089S
KS096S	WHP	1.000	0.000	0.444	0.235	0.286	0.375	0.462	0.471	0.471	0.267	0.231	0.171	0.065
NE086S	WHP	0.000	1.000	0.250	0.125	0.400	0.267	0.333	0.125	0.250	0.286	0.080	0.000	0.000
NE094S	WHP	0.444	0.250	1.000	0.286	0.333	0.308	0.400	0.143	0.429	0.333	0.087	0.000	0.000
NE081S	WHP	0.235	0.125	0.286	1.000	0.308	0.286	0.333	0.000	0.273	0.300	0.323	0.300	0.222
NE096S	WHP	0.286	0.400	0.333	0.308	1.000	0.400	0.273	0.308	0.462	0.500	0.286	0.182	0.150
KS078S	CGP	0.375	0.267	0.308	0.286	0.400	1.000	0.588	0.667	0.762	0.737	0.467	0.256	0.286
KS097S	CGP	0.462	0.333	0.400	0.333	0.273	0.588	1.000	0.444	0.444	0.500	0.296	0.167	0.125
KS100S	CGP	0.471	0.125	0.143	0.000	0.308	0.667	0.444	1.000	0.545	0.400	0.323	0.250	0.222
NE077S	CGP	0.471	0.250	0.429	0.273	0.462	0.762	0.444	0.545	1.000	0.600	0.516	0.300	0.333
NE080S	CGP	0.267	0.286	0.333	0.300	0.500	0.737	0.500	0.400	0.600	1.000	0.414	0.211	0.235
KS081S	FH	0.231	0.080	0.087	0.323	0.286	0.467	0.296	0.323	0.516	0.414	1.000	0.490	0.533
KS085S	FH	0.171	0.000	0.000	0.300	0.182	0.256	0.167	0.250	0.300	0.211	0.490	1.000	0.741
KS089S	FH	0.065	0.000	0.000	0.222	0.150	0.286	0.125	0.222	0.333	0.235	0.533	0.741	1.000

Table 3. Partial Sørensen similarity matrix (Omernik Level III Ecoregions). WHP=western high plains; CGP=central great plains; FH=flint hills

Trophic Guilds	
Guild Code	Description
B_GEN	benthic generalist
INVPISC	invertivore and piscivore
INV	Invertivore
B_INV	benthic invertivore
INSECTIV	Insectivore
B_INS	benthic insectivore
B_MICOMNI	benthic microphagic omnivore
B_MACOMNI	benthic macrophagic omnivore
MICOMNI	microphagic omnivore
MACOMNI	macrophagic omnivore
PISC	piscivore/top carnivore
B_HERB	benthic herbivore
FILTERER	filter feeder
PLANKTIV	Planktivore

Reproductive Guilds	
Guild Code	Description
LITHO_A1	non-guarding open substrate spawner
LITHO_A2	non-guarding eggs buried spawner
PHYTO_A1	non-guarding eggs broadcast on veg.
LITHO_B1	guarding eggs attached to rocks
LITHO_B2	guarding eggs laid in nest
PHYTO_B1	guarding eggs attached to veg.
PHYTO_B2	guarding eggs in nest of plant material
NESTASSO	nest associated
BEARERC2	live bearer

Table 4. Trophic and reproductive guilds used to define reference stream fish communities from Kansas, Nebraska and Missouri. Guilds employed here to classify fish were based on those used by the USEPA Regional Environmental Monitoring and Assessment Program (REMAP). The REMAP program used reproductive guilds defined by Balon (1975). The highlighted guilds were not found in the wadeable reference streams analyzed for this study.

	Sorensen Index (Presence/Absence)	Bray-Curtis Index (Relative Abundance)
Stream Classification Approaches	G>B=O~H>M>HO>>HB>>RHO~THB>RHB~THO>S	O~B>HO~M=HB~H>G>>THB~S>THO>RHB~RHO

Table 5. Rankings of the % maximum CS values for stream classification approaches in the four-state area. O = Omernik Level III ecoregions, B = Bailey sections, M = Maxwell et al. river basins, G = small geographic distance clusters, S = Strahler stream order, H = 4-digit hydrologic unit codes (HUCs). HB and HO represent Hybrid regions created for this study, which combine the ecoregion and watershed designs. HB = Bailey province stratified by 2-digit HUC, HO = Omernik level II ecoregion stratified by 2-digit HUC, RHO and THO = HO regions analyzed using fish reproductive guilds and trophic guilds respectively, and RHB and THB = HB regions analyzed using fish reproductive guilds and trophic guilds respectively. Trophic and reproductive guilds were analyzed over three states (Kansas, Missouri and Nebraska).

Ecoregion by HUC Hybrid regions - Species Analysis	% of maximum attainable CS (S.I.)	% of maximum attainable CS (B.C.I)	Ecoregion by HUC Hybrid regions - Func. Group Analysis	% of maximum attainable CS (S.I.)	% of maximum attainable CS (B.C.I.)
2-digit HUCS/Bailey Province	56	50	Trophic Groups 2-digit HUCS/Bailey Province	38	29
2-digit HUCS/Omernik Level II	68	51	Trophic Groups 2-digit HUCS/Omernik Level II	34	21
Subanalysis 2-digit HUCS/Bailey Province	65	37	Repro. Groups 2-digit HUCS/Bailey Province	35	15
Subanalysis 2-digit HUCS/Omernik Level II	55	28	Repro. Groups 2-digit HUCS/Omernik Level II	40	13

Table 6. Comparison of the % of the maximum Classification Strength (CS) for Hybrid Regions based on species vs functional groups. CS values were based on similarities among stream communities defined by fish species composition, trophic functional guilds and reproductive functional guilds. The subanalysis was a repeat of the species analysis performed on the subset of sites that were used in the functional group comparisons.

			Sorensen Similarities (Presence/Absence)					**Bray-Curtis Similarities (Relative Abundance)**				
Group Name	No. of Groups	No. of Streams	Overall mean similarity within groups (W_i)	Mean similarity among groups (B)	Class. Strength (CS)%	B/W	% of maximum attainable CS	Overall mean similarity within groups (W_i)	Mean similarity among groups (B)	Class. Strength (CS)%	B/W	% of maximum attainable CS
Species 2-digit HUCS/Bailey Province	8	220	0.46	0.34	12.4	0.73	56	0.20	0.12	8.3	0.59	50
Species 2-digit HUCS/Omernik Level II	8	221	0.45	0.30	15.5	0.66	68	0.20	0.12	8.4	0.58	51
Subanalysis 2-digit HUCS/Bailey Province	6	62	0.45	0.29	15.4	0.65	65	0.18	0.11	7.1	0.60	37
Subanalysis 2-digit HUCS/Omernik Level II	5	61	0.42	0.30	11.6	0.72	55	0.16	0.11	4.7	0.71	28
Trophic Groups 2-digit HUCS/Bailey Province	6	62	0.74	0.67	6.9	0.91	38	0.28	0.22	6.1	0.78	29

Trophic Groups 2-digit HUCS/Omernik Level II	5	61	0.72	0.67	5.0	0.93	34	0.27	0.23	4.0	0.85	21
Repro. Groups 2-digit HUCS/Bailey Province	6	62	0.82	0.76	5.7	0.93	35	0.32	0.28	3.9	0.88	15
Repro. Groups 2-digit HUCS/Omernik Level II	5	61	0.82	0.77	5.3	0.93	40	0.31	0.28	3.1	0.90	13

Table 7. Classification Strengths (CS) for Hybrid Regions. CS values were based on similarities among stream communities defined by fish species composition, trophic functional guilds and reproductive functional guilds. The subanalysis was a repeat of the species analysis performed on the subset of sites that were used in the functional group comparisons.

Taxonomic Unit	Number of CS values used to find the average % of the maximum CS	Watershed divided by Ecoregions (S.I.)	Watershed divided by Ecoregions (B.C.I.)	Ecoregion divided by Watersheds (S.I.)	Ecoregion divided by Watersheds (B.C.I.)
Trophic Functional Groups	2 to 3	35	46	39	34
Repro. Functional Groups	2	16*	3*	42	17*
Species	2	69	46	83	58
Species (Subanalysis)	2	NA	NA	76	49

Table 8. Average results from Classification Strength (CS) analyses of ecoregions and watersheds nested within each other. From the hybrid maps, different ecoregions that run through the same watershed were identified, and a CS analysis was performed on just this area where the ecoregions and one specific watershed intersect. The same analysis was performed on areas where different watersheds run through the same ecoregion. The analyses were performed using both fish functional groups and species to define communities. Trophic and reproductive functional groups were based on functional groups in Table 4. The species analysis included all sites from the region being analyzed from the original matrix of 231 sites. The species subanalysis used only the same sites that were used in the functional group analyses. B-C indicates that the Bray-Curtis similarity analysis was used to calculate the % Maximum CS. Sor indicates that the Sorensen similarity analysis was used to calculate the % maximum CS. The asterisk indicates that at least one permutation test resulted in a non-significant p value.

Watershed divided by Ecoregions	No. of Groups	No. of Streams	% of maximum attainable CS (Sor)	% of maximum attainable CS (B-C)		Ecoregion divided by Watersheds	No. of Groups	No. of Streams	% of maximum attainable CS (Sor)	% of maximum attainable CS (B-C)
(trophic gps) Omer ecoregions 9.3,9.4,9.2,8.4 within Mo. 2-digit HUC	4	52	41	17		(trophic gps) Mo and AWR watersheds within 9.4 Omer Ecoregion	2	29	28	21
(trophic gps) Bailey ecoregions GPP,GPSP, PP, EBF within Mo. 2-digit HUC	4	52	37	23		(trophic gps) Mo and AWR 2-digit HUCs within Bailey ecoregion GPSP	2	18	51*	46
(trophic gps) Bailey ecoregions GPSP and PP within AWR 2-digit HUC	2	10	27	100		(repro gps) Mo and AWR 2-digit HUCs within Bailey ecoregion GPSP	2	18	53	50*
(repro gps) Bailey ecoregions GPSP and PP within AWR 2-digit HUC	2	10	3*	-1*		(repro groups) Mo and AWR Watersheds in Bailey Prairie Parkland	2	28	32	-15*
(repro gps) Omer ecoregions 9.3,9.4,9.2,8.4 within Mo. 2-digit HUC	4	52	28	8*						

Table 9A. Individual CS values (using functional guilds) from the analysis of ecoregions and watersheds nested within each other. $p < 0.05$ unless denoted by *.

Watershed divided by Ecoregions	No. of Groups	No. of Streams	% of maximum attainable CS (Sor)	% of maximum attainable CS (B-C)		Ecoregion divided by Watersheds	No. of Groups	No. of Streams	% of maximum attainable CS (Sor)	% of maximum attainable CS (B-C)
(Spp) Omer ecoregions 9.3,9.4,9.2,8.4 within Mo. 2-digit HUC	4	110	46	33		(Spp) Omer ecoregion 9.2 by AWR, Missi. & Mo. 2-digit HUC	4	117	100	59
(Spp) Omer ecoregions 9.2 and 8.1 within upper Missi. 2-digit HUC	2	69	91	58		subanalysis (Spp) Mo and AWR Watersheds in Bailey ecoregion GPSP	2	18	100	68
						subanalysis (Spp) Mo and AWR Watersheds in Omer ecoregion 9.4	2	29	52	30
						(SPP) Omer 9.2 by AWR and MO	2	60	67	56

Table 9B. CS values (using species) from the analysis of ecoregions and watersheds nested within each other.

	No. of Groups	No. of Streams	% of maximum attainable CS (Sor)	% of maximum attainable CS (B-C)
(Spp) ecoregion 8.1 in Upper Missi.2-digit HUC compared to 9.2 in AWR 2-digit HUC	2	20	100	97

Table 9C. CS values from a comparison of streams that are both in different watersheds and in different ecoregions. This differs from the above anayses in Tables 9A and 9B, which are comparisons of streams that share the same watershed or that share a common ecoregion.

Regional Division Number and Description	No. of Groups	No. of Streams	% of maximum attainable CS (S.I.)	% of maximum attainable CS (B.C.I.)	Comments
#1 (Spp) ecoregion 8.1 in Upper Missi.2-digit HUC compared to 9.2 in AWR 2-digit HUC	2	20	100	97	diff. watersheds diff. ecoregions sections not adjacent
#2 (Spp) Upper Missi. 2-digit HUC divided by ecoregions 9.2 and 8.1	2	69	91	58	same watershed diff. ecoregions sections are adjacent
#3 (Spp) ecoregion 9.2 divided by Upper Missi. and AWR 2-digit HUCs	2	65	100	100	diff. watersheds same ecoregion sections not adjacent
#4 (Spp) ecoregion 9.2 divided by AWR and MO 2-digit HUCs	2	60	67	56	diff. watersheds same ecoregion sections are adjacent

Table 10. Classification strength values for the analysis examining the combined effect of being located in different ecoregions and different watersheds on streams. The inclusion of regional comparisons in which regions are adjacent and not adjacent elucidates the impact of spatial proximity relative to ecoregion or watershed effect. CS values were based on species community similarity (Spp). Only Omernik ecoregions were used in this analysis. See Figure 5 for the hybrid Omernik/HUC map. AWR=Arkansas White Red, MO=Missouri.

Cluster 1		Cluster 2		Cluster 6	
Count	26	Count	12	Count	23
Sum_Litho_b2	100	Sum_Litho_b2	100	Sum_Litho_b1	100
Sum_Phyto_a1	100	Sum_Litho_a1	92	Sum_Litho_b2	100
Sum_Nestasso	96	Sum_Litho_b1	92	Sum_Nestasso	100
Sum_Litho_a1	77	Sum_Litho_a2	75	Sum_Litho_a1	96
Sum_Litho_a2	69	Sum_Phyto_a1	67	Sum_Litho_a2	61
Sum_Litho_b1	62	Sum_Bearerc2	0	Sum_Bearerc2	39
Sum_Phyto_b1	8	Sum_Nestasso	0	Sum_Phyto_a1	30
Sum_Bearerc2	4	Sum_Phyto_b1	0	Sum_Phyto_b1	0
Sum_Phyto_b2	0	Sum_Phyto_b2	0	Sum_Phyto_b2	0

Table 11. Percentages of streams occupied by each reproductive fish guild within three maximum similarity clusters. The clusters were based on similarity among reproductive fish guild composition (Sorensen Index).

Cluster1		Cluster3		Cluster6	
Count	12	Count	27	Count	22
Sum_Bmacomni	100	Sum_Bins____	100	Sum_Bins____	100
Sum_Invpisc_	100	Sum_Invpisc_	100	Sum_Bmacomni	100
Sum_Inv_____	67	Sum_Ins_____	93	Sum_Invpisc_	95
Sum_Macomni_	67	Sum_Bherb___	89	Sum_Inv_____	91
Sum_Bins____	50	Sum_Bmacomni	85	Sum_Bgen____	55
Sum_Binv____	33	Sum_Macomni_	81	Sum_Bherb___	45
Sum_Bgen____	17	Sum_Inv_____	70	Sum_Ins_____	45
Sum_Bmicomni	17	Sum_Binv____	59	Sum_Micomni_	36
Sum_Micomni_	8	Sum_Bgen____	30	Sum_Pisc____	32
Sum_Pisc____	8	Sum_Bmicomni	19	Sum_Macomni_	23
Sum_Bherb___	0	Sum_Micomni_	11	Sum_Binv____	18
Sum_Ins_____	0	Sum_Pisc____	4	Sum_Bmicomni	18

Table 12. Percentages of streams occupied by each trophic fish guild within three maximum similarity clusters. The stream clusters were based on similarity among trophic fish guild composition (Sorensen Index).

	Sorensen Index	Bray-Curtis Index
Species	EW	EW
Reproductive Guilds	EW	*
Trophic Guilds	EW	WE

Table 13. The performance of the watershed divided by ecoregions (WE) compared to the ecoregion divided by watersheds (EW). Based on the classification strength analysis, the top-performing regional divisions were listed in the appropriate cell according to the index and type of community used in the analysis. The asterisk indicates that the regional divisions analyzed did not perform better than a random reassignment of sites to groups ($p>0.05$).

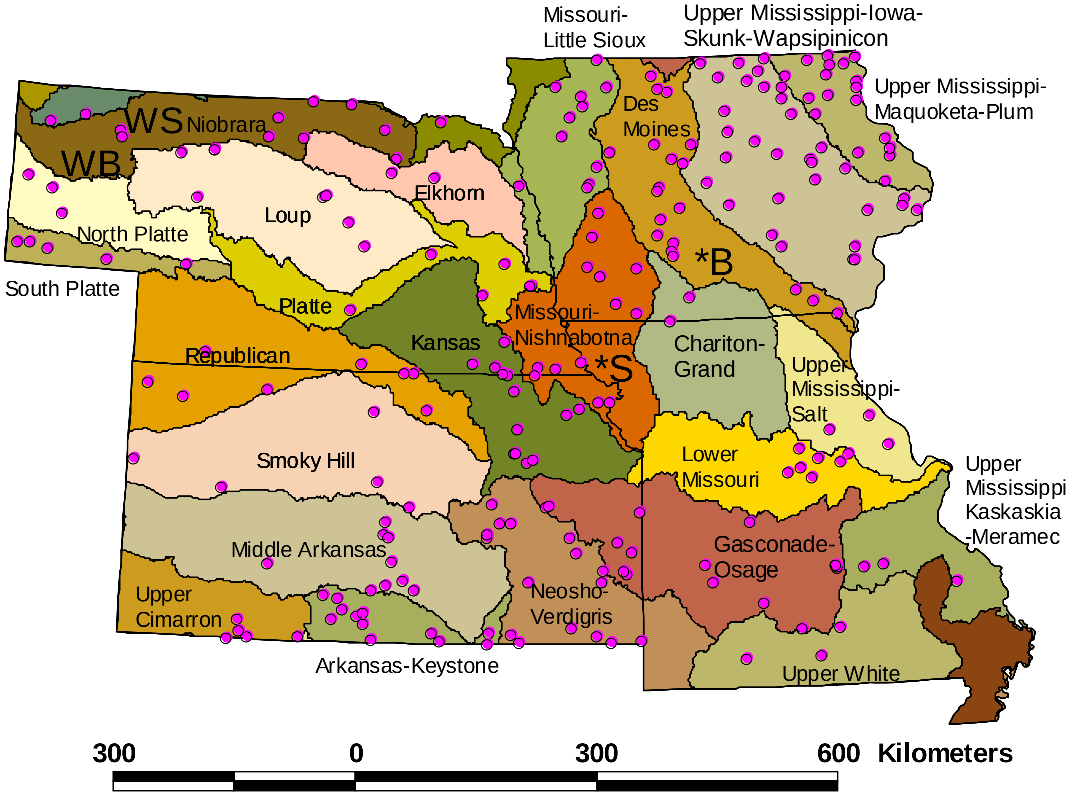


Figure 1. 4-digit HUCs within the 4-state study area with reference sites

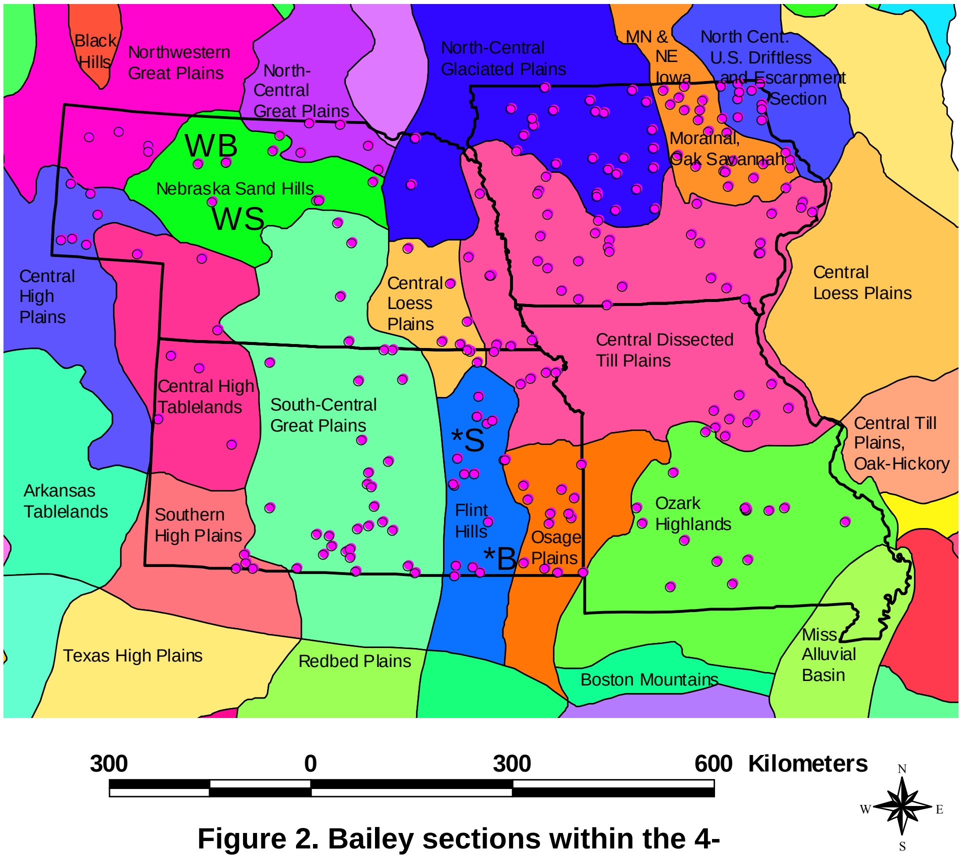
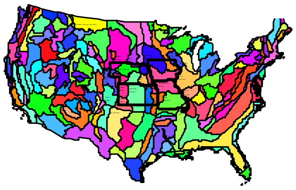


Figure 2. Bailey sections within the 4-state study area with reference sites



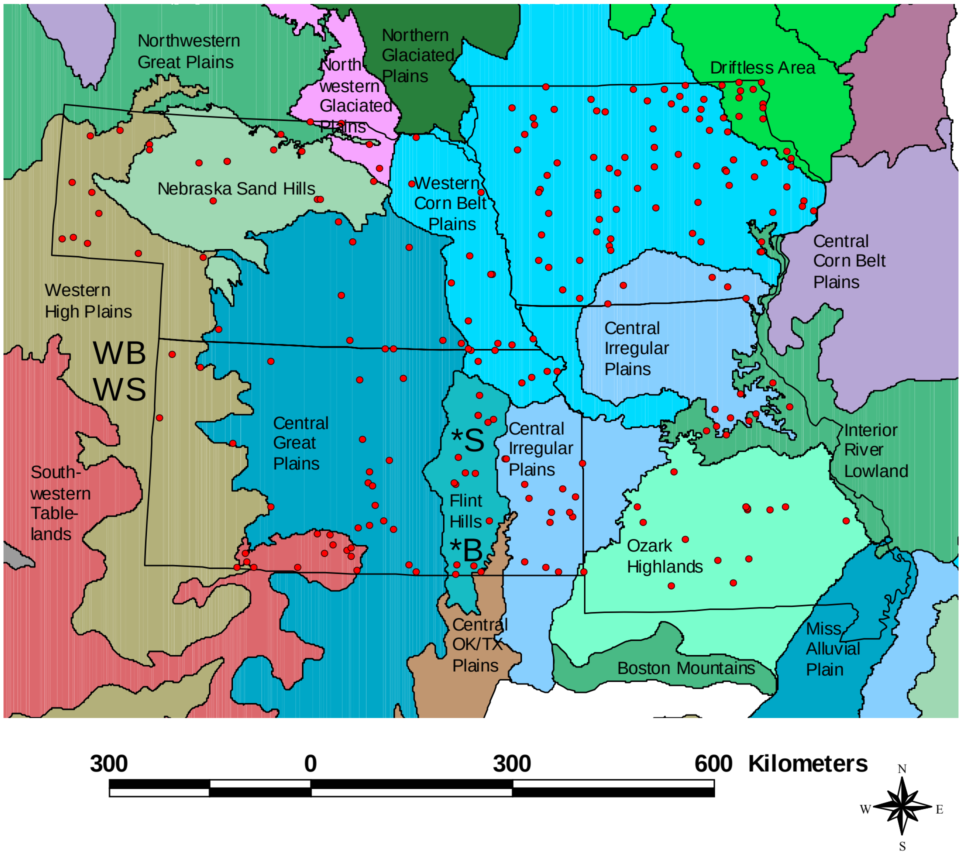


Figure 3. Omernik level III ecoregions within the 4-state study area with reference sites

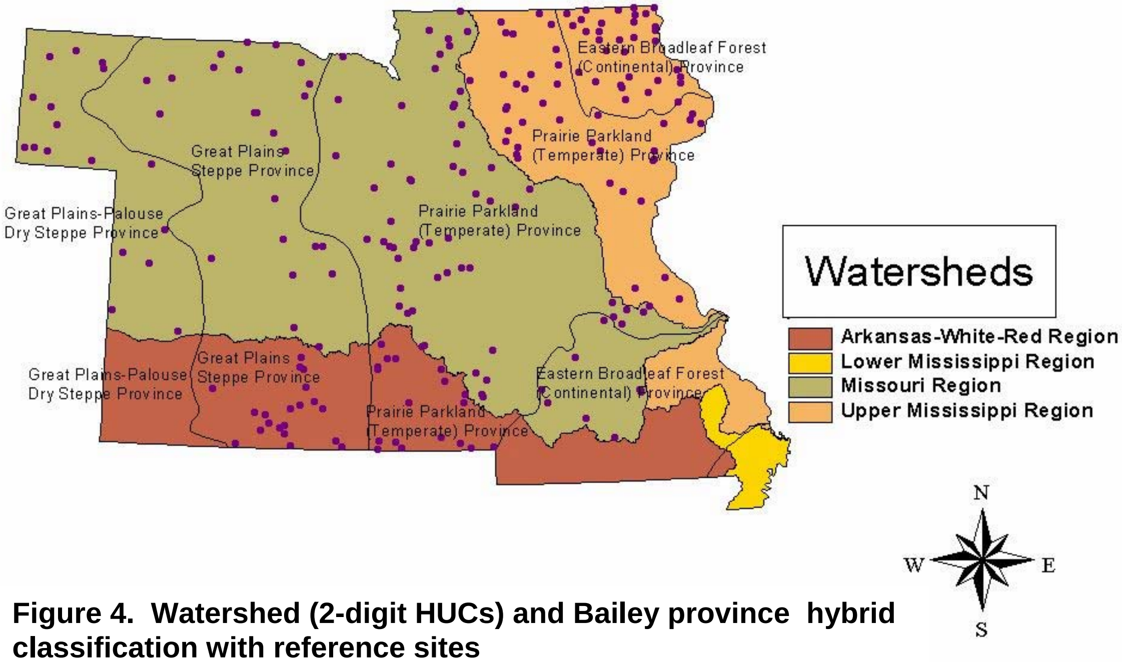


Figure 4. Watershed (2-digit HUCs) and Bailey province hybrid classification with reference sites

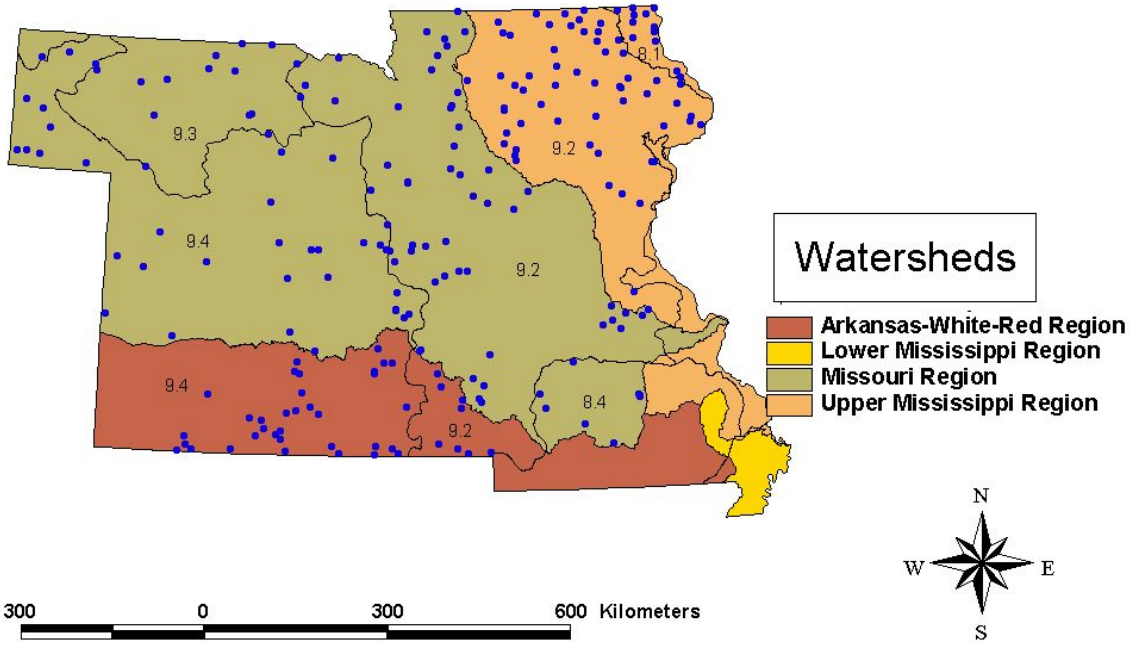


Figure 5. Watershed (2-digit HUCs) and Omernik level II ecoregion hybrid classification with reference sites

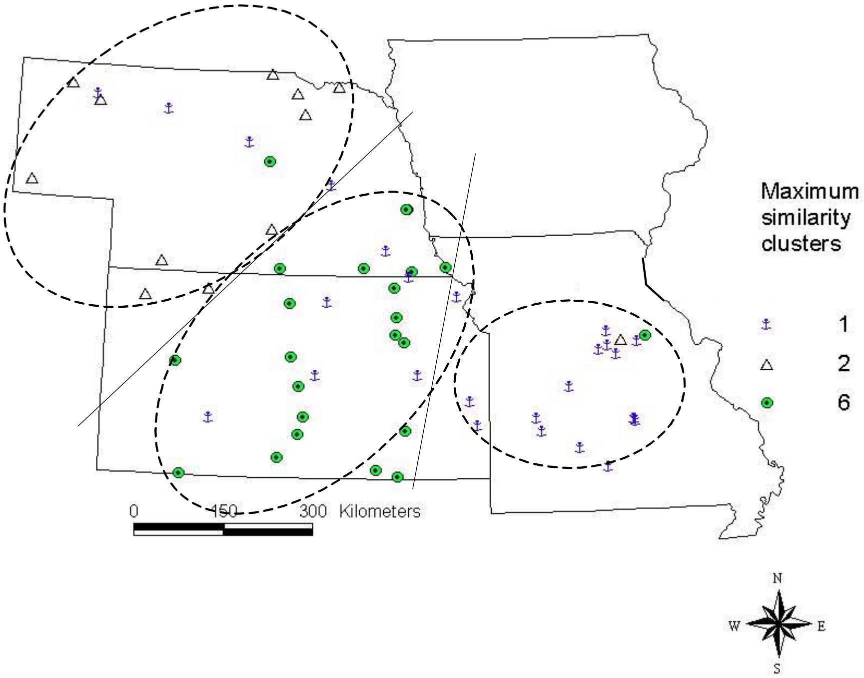


Figure 6. Reproductive guild community clusters based on the Sorensen Index over three states. The clusters with the strongest geographic affinities are circled. Lines represent divisions between distinct regions of similar types of reproductive guild communities, indicating a potential gradient in influential environmental conditions from the Southeast to the Northwest.

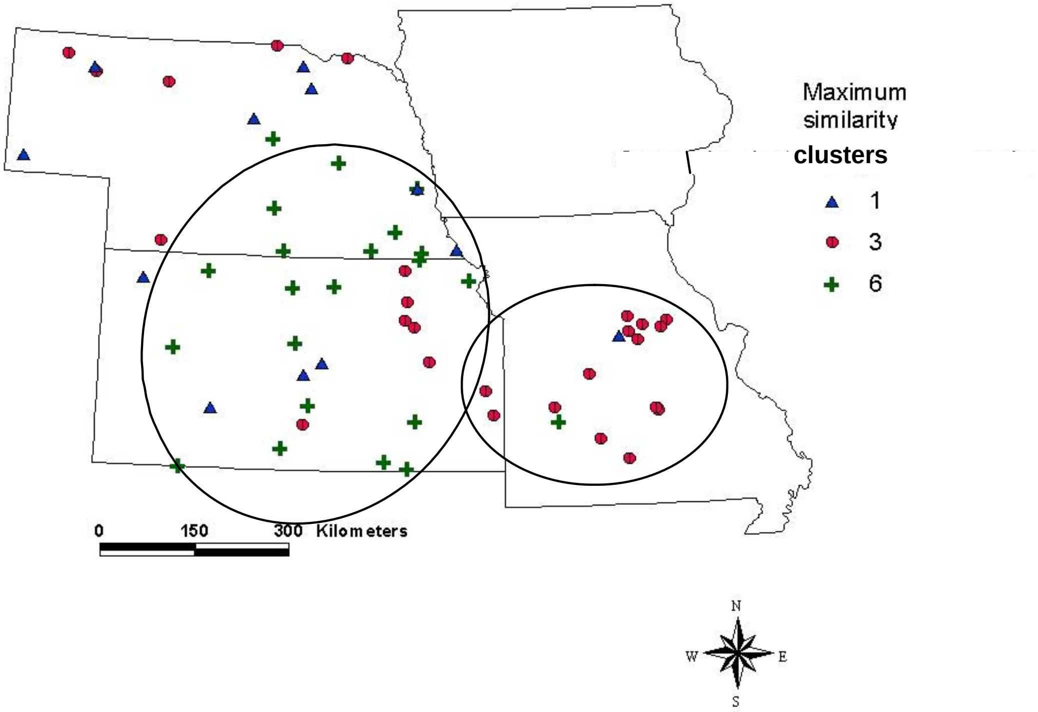


Figure 7. Trophic guild community clusters based on the Sorensen Index over three states. The clusters with the strongest geographic affinities are circled.

Appendix for Chapter 2

			Sorensen Similarities (Presence/Absence)					Bray-Curtis Similarities (Relative Abundance)				
Group Name	No. of Groups	No. of Streams	Overall mean similarity within groups (W_i)	Mean similarity among groups (B)	Class. Strength (CS)%	B/W	% of maximum attainable CS	Overall mean similarity within groups (W_i)	Mean similarity among groups (B)	Class. Strength (CS)%	B/W	% of maximum attainable CS
2-digit HUCS/Bailey Province	8	220	0.46	0.34	12.4	0.73	56	0.20	0.12	8.3	0.59	50
2-digit HUCS/Omernik Level II	8	221	0.45	0.30	15.5	0.66	68	0.20	0.12	8.4	0.58	51
Subanalysis 2-digit HUCS/Bailey Province	6	62	0.45	0.29	15.4	0.65	65	0.18	0.11	7.1	0.60	37
Subanalysis 2-digit HUCS/Omernik Level II	5	61	0.42	0.30	11.6	0.72	55	0.16	0.11	4.7	0.71	28
Trophic Groups 2-digit HUCS/Bailey Province	6	62	0.74	0.67	6.9	0.91	38	0.28	0.22	6.1	0.78	29
Trophic Groups 2-digit HUCS/Omernik Level II	5	61	0.72	0.67	5.0	0.93	34	0.27	0.23	4.0	0.85	21

Repro. Groups 2-digit HUCS/Bailey Province	6	62	0.82	0.76	5.7	0.93	35	0.32	0.28	3.9	0.88	15
Repro. Groups 2-digit HUCS/Omernik Level II	5	61	0.82	0.77	5.3	0.93	40	0.31	0.28	3.1	0.90	13
2-digit HUCS/Bailey Province Fish Clusters	8	218	0.51	0.29	22.3	0.56		0.27	0.10	16.6	0.38	
2-digit HUCS/Omernik Level II Fish Clusters	8	221	0.51	0.28	22.8	0.55		0.27	0.10	16.5	0.39	
Subanalysis 2-digit HUCS/Bailey Province Fish Clusters	6	62	0.51	0.28	23.7	0.54		0.28	0.09	19.0	0.32	
Subanalysis 2-digit HUCS/Omernik Level II Fish Clusters	5	61	0.49	0.28	21.1	0.57		0.25	0.08	16.8	0.32	

Trophic groups2-digit HUCS/Bailey Province Fish Clusters	6	62	0.82	0.63	18.4	0.78		0.38	0.17	21.1	0.45	
Trophic groups2-digit HUCS/Omernik Level II Fish Clusters	5	61	0.78	0.64	14.7	0.81		0.36	0.17	19.1	0.47	
repro groups2-digit HUCS/Bailey Province Fish Clusters	6	62	0.92	0.76	16.1	0.83		0.50	0.24	26.5	0.47	
repro groups2-digit HUCS/Omernik Level II Fish Clusters	5	61	0.87	0.74	13.2	0.85		0.47	0.22	24.4	0.48	

Appendix Table A. Classification Strengths (CS) for Ecoregion/HUC Hybrid Regions. CS values were based on similarities among stream communities defined by fish species composition, trophic functional guilds and reproductive functional guilds. The subanalysis was a repeat of the species analysis performed on the subset of sites that were used in the functional group comparisons. Maximum similarity clusters are shaded.

CHAPTER THREE

Patterns in historical fish communities and homogenization in Midwest streams

Introduction

The first two chapters of this dissertation revealed moderately weak regional affinities between reference stream fish communities and regional classifications such as ecoregions and watersheds in Kansas, Missouri, Nebraska and Iowa. Since ecoregions and watersheds represent areas that contain distinct environmental attributes (e.g., soil type or patterns in run-off), which should influence fish community composition, this weak correspondence suggests that fish faunas in the study area have become homogenized. In other words, species turnover, or beta diversity among stream fish assemblages in different watersheds or ecoregions was likely higher in the past than the beta diversity revealed by the modern stream fish data. In essence, we are not losing or gaining as many different species as we move from region to region as we did in the past. This is called biotic homogenization.

The phenomenon of biotic homogenization is a world-wide dilemma (Arthington 1991; Lodge et al. 2000 and Lockwood and McKinney 2001). Some scientists have come to regard the next epoch as the "Homogecene" because of the dramatic decline in regionally and globally unique species assemblages (Guerrant

1992). The paradox of homogenization is that it may cause an increase in diversity locally (alpha diversity) due to invasion and range expansion of nonnatives or generalist species in the neighboring habitats, but a likely decrease in global diversity eventually due to the extinction of certain endemics and specialists (Rahel 2000). Homogenization may have many causes, such as: habitat destruction; building of impoundments; pollution; introduction of non-natives through bait buckets, ballast water, etc.; removal of integral species that other fish species depend on in an ecosystem. Extinction can result from any of the above.

Scientists have noted that we have combined and expunged distinctive communities of species that have historically inhabitted streams of the central part of the Midwest (Cross and Moss 1987 and Pfleiger and Grace 1987). However, there has been little work done to quantify the degree of homogenization of freshwater stream communities since humans first began major channelization, filling, and impoundment building in the area (post 1950). It is also unclear how much impact physical boundaries to dispersal once had on fish species distributions in the Midwest. In other words, it is unclear whether watersheds were characterized by communities and species that were very distinct from neighboring watersheds.

This study attempts to quantify overall homogenization of fish communities among watersheds (represented here by 4-digit HUCs) in one state in the central Midwest (Kansas) and examine finer scale homogenization among pairs of watersheds by comparing historic stream communities (pre 1958) to modern stream communities (post 1988). The study utilized historical survey data from the Kansas

University Natural History museum and the Kansas Biological Survey to reconstruct assemblages of Kansas stream fish species of the past (pre-1958), which were likely not yet strongly impacted by the major reservoir projects of the 1950's and 1960's. These stream faunas of the past were then compared to modern Kansas reference stream faunas constructed from the dataset used in the previous studies described in chapters one and two. The use of the reference stream data to represent modern stream faunas provided the most conservative test for homogenization in the study area, because of the decreased likelihood that invasive species were present in the reference streams. Therefore, the homogenization estimate provided by this study was likely equal to the minimum homogenization that has occurred in the Kansas watersheds.

One challenge to this type of analysis was that the data (fish species) from the two different time periods were collected differently. The modern samples were quantitative (presence-absence or abundance data), and the past samples were qualitative or "incidence-based" samples. Therefore, in order to compare these datasets, the data had to be converted to incidence-based data, and only the watersheds with the most accurate assessments of species richness or diversity were included in the analyses. The accuracy of the species richness assessment based on the past and modern data was calculated with a completeness ratio based on the number of species present in the samples over an estimate of the actual number of species present using the Incidence Coverage Estimation algorithm (Colwell 1997). From this assessment, a subset of five watersheds within Kansas was chosen for the homogenization analysis rather than all nine present in the state. Those watersheds included in this assessment were: the Gasconade-Osage, the Neosho-Verdigris, the Smoky Hill, the Kansas and the Upper Cimarron watersheds (see Figure 1 for a map).

Homogenization is often measured as a decrease in beta diversity or, logically, an increase in β similarity (Magurran 2003). In this study, overall mean similarity (as calculated by the Sorensen and Jaccard similarity indices) among stream fish assemblages in watersheds of the past (pre 1958) was compared to the mean similarity of assemblages among watersheds currently (post 1988). The difference between these mean similarities provided a coarse-grain quantification of the amount of homogenization that has occurred among watersheds in the state of Kansas since the 1950's. In addition, similarity among each pair of watersheds in the past was compared to similarity among those same two watersheds currently to identify watershed pairs that have suffered particularly severe homogenization, or, in contrast, to identify pairs that have been less-affected by homogenizing forces (e.g., translocations, extirpations, etc.). The analyses above will also indicate the extent to which physical boundaries to dispersal shaped historic fish distributions in Kansas relative to their influence on current fish community patterns. Community similarity indices were also used to compare the past and present assemblages within the same watershed in order to quantify the change in the fish community that has occurred temporally within individual watersheds in Kansas. Finally, two types of ordinations (Detrended Correspondence Analysis and Non-metric Multidimensional scaling) of the watershed assemblages were performed to provide two additional alternative methods for assessing the similarity of these communities to each other.

In an applied context, a useful outcome from this kind of study is that it could serve to inform the development of more accurate reference stream conditions. If homogenization of stream communities over time is quantified, this can provide a reliable indication of how distant our “reference condition” (or least disturbed condition) may be from truly undisturbed conditions. Scientists and managers can attain a better understanding of how close the “best attainable” stream condition is to the past diversity that was once represented at the regional scale. At the very least, this kind of information can serve as a caveat to the reference conditions that the management community uses in regulation.

Materials and Methods

This study attempted to quantify the amount of homogenization that has occurred among stream fish assemblages at the watershed scale (4-digit HUCs-hydrologic unit codes) in the state of Kansas. Essentially, the goal was to assess whether there was in fact an increase in βsimilarity among watersheds that would indicate homogenization among watershed faunas since the beginning of major modifications to stream systems in Kansas (since the 1950’s). The watershed was also preferred by Rahel (2000) as the geographic unit to compare in his assessment of the homogenization of U.S. fish faunas, but he had to conduct his analysis at the state scale because of a lack of data at the watershed scale.

There were two major datasets employed in this study, which will be called "past" and "modern." The past dataset contained fish data from wadeable streams collected before 1958, and was from the Kansas University Natural History Museum and the Kansas Biological Survey. By using data before 1958, the influence of major reservoir projects, large-scale channelization, large-scale urbanization, road-building and introductions of non-natives was minimized. The use of pre-1958 data allowed the study to assess the homogenizing impact of these major anthropogenic changes on fish communities. The past data were compared to the modern fish community data, which was essentially the Kansas subset of the four-state database containing wadeable reference streams that was used in the first two studies of ecoregions and fish communities within this dissertation (Chapters one and two).

The past data can be regarded as museum collection data. The data years ranged from 1885 to 1957, and records from all 9 watersheds within the state of Kansas were included in the database. The data needed to be extensively culled and reformatted in order to be used in this study. Fish found in lakes and ponds, and fish only identified to genus, were culled out of the database, which originally contained 3,367 individual fish records. Also, out-of-date or synonymous taxa had to be renamed so the historic and modern datasets could be compared. For example, data had to be merged that were associated with the synonyms of the duskystripe shiner (*Luxilus pilsbryi* and *Notropis pilspryi*), which are both included in the museum data, into one column under the current name, *Luxilus pilsbryi*. Also for the museum data, the old name for the speckled chub (*Extrarius aestivalis)* was replaced with its current epithet, *Macrhybopsis aestivalis*. Three marine species were also identified as mistakes in the dataset and removed (e.g., herring, or *Clupea harengis*)! From the database of records, communities were reconstructed based on their field number, which corresponded to a single site on a single sampling day. After records were grouped by field number (the field number can essentially be regarded as the "sample unit"), there were 638 samples in the past dataset. The georeferenced data were converted from minutes and seconds into decimal degrees, uploaded into ArcView and overlaid on maps of geographical classifications (i.e., 4-digit HUCs, or watersheds). The samples were then grouped by watershed. Those samples that were not georeferenced (77 samples in all) were assigned to watersheds if the county they were in fell completely within a single watershed. After culling all samples that could not be assigned to a watershed, the presence or incidence data were used to construct a sample (field number) by species matrix (623 samples by 120 species) with a total of that could be analyzed directly, or from which species lists could be generated for each watershed.

The past data were not consistently quantitatively sampled. Some samples from a single sampling day at one site consisted of one specimen, while others contained 13 or more species. Sampling methods ranged from a single seine along a reach of a stream, to several seines of representative habitats in a stream, to a single kick-net sample, to applying rotenone over an entire stream reach and collecting all the fish that died (Frank Cross pers. comm.). Also, multiple individuals were generally not taken, so abundance data was not generally available.

The modern data, however, were quantitatively sampled, as described in Chapters one and two. Therefore, many more individuals were collected, and many more species were collected per sample – total number of samples was 81, but the total number of individuals was 84,937. Since the modern dataset was sampled quantitatively, and the past dataset was not, all of the samples were converted to incidence, or presence-absence, data (two matrices of samples by species filled with ones and zeroes). This was done in a recent study by Longino et al. (2001), who were comparing similarly varied datasets.

Due to the challenge of comparing past museum collection data to modern agency-collected data, the most prudent initial measurement of similarity among watersheds should come from a comparison of species lists created from the samples rather than the individual samples themselves. Because the datasets were different, it was also important to assess whether there were watersheds with diversity that was severely underestimated in either of the datasets. The diversity within the watersheds is termed alpha diversity (the richness within the watershed "habitat"). In order to have a meaningful analysis, watersheds that are compared should have species accumulation curves that are near saturation – indicating that the samples collected have accurately depicted the diversity in an area. These species accumulation curves were generated in PC-ORD for Windows (version 4.20, 1999, MjM software, Gleneden Beach, Oregon) using a smoothing algorithm, which randomly resamples the data one hundred times (without replacement), and assigns confidence intervals to the curves (see Figure A in the appendix for an example of a species accumulation curve generated for the Gasconde-Osage watershed). Essentially, the program produces a rarefaction curve (also called a randomized species accumulation curve), which can be seen as the statistical representation of the actual species accumulation curve (Gotelli and Colwell 2001).

In addition, the completeness of the species list in each watershed was estimated by using the Incidence Coverage Estimation (ICE) (Colwell 1997) algorithm as calculated by the EstimateS statistical package (Colwell 2005), which estimates the true number of species based on the growth of the species list from sample to sample. This estimator was specifically chosen because the extrapolation algorithm does not require abundance data, and is not affected by sample size. The ratio of the observed species (S_{obs}) in the sample to the estimated number of species (S_{est}) will provide an estimation of the proportion of "true" diversity in the watershed that is included in the datasets used in the analysis. The ratio of Sobs/Sest is called the completeness ratio, and was used by Soberon et al. (2000) to estimate the completeness of the alpha diversity characterized by a museum database of butterflies at several geographic scales. Those watersheds not reaching at least 80% completeness were excluded from this analysis. Those watersheds with completeness ratios over 80% were: the Gasconade-Osage, the Kansas, the Neosho-Verdigris, the Upper Cimarron and the Smoky Hill watersheds. These were the five watersheds included in the analysis.

The measurement of homogenization

Since homogenization is essentially an increase in the similarity of spatially distinct biotas over time, it is recommended that similarity indices be used to quantify that homogenization (Rahel 2002).

β similarity (inversely related to beta diversity) among pairs of watersheds were calculated using two different indices that are based on presence-absence data. These presence/absence similarity indices are: the Sorensen index (Sørensen 1948) and the Jaccard index.

The Sørensen index (S.I.) is as follows:

$$\text{S.I.} = 2c/(s_1+s_2) \qquad \text{Eq. 1}$$

Where s_1 is the number of species in community 1; s_2 is the number of species in community 2; c is the number of species both communities have in common.

The Jaccard index (J.I.) is as follows:

$$\text{J.I.} = (a/(a+b+c)) \qquad \text{Eq. 2}$$

where a=number of spp present in both habitats (biotas); b=the number of species present in only the first habitat (biota); c=number of species present only in the second habitat (biota) (Radomski and Goeman 1995, Marchant et al. 2001).

The Jaccard and Sorensen indices are widely used similarity indices. The Sorensen similarity index has been used to indicate β similarity as a valid (inverse) descriptor of beta diversity (Magurran 2003) – the higher the β similarity, the lower the beta diversity. In addition, Rahel (2000) used the jaccard similarity index in his study of the homogenization of fish fauna among U.S. states. This method provides two different formulas for calculating similarity among watersheds that can be used to corroborate or refute the results.

In order to quantify homogenization over all the watersheds assessed here (coarse-grain picture of homogenization), the overall mean similarity among watersheds in the past was subtracted from the overall mean similarity among watersheds from the modern data. A paired t-test was conducted to evaluate the significance of the difference between the past and present beta-similarities. In addition, a Mantel test was done to evaluate whether the pattern of similarity among pairs of watersheds in the past was related to the pattern seen in pairs of watersheds today. This is a statistical test that compares two matrices of similarities or dissimilarities by computing the sum of the cross-products of the matrices. The Mantel test compares whether the distances between elements in one matrix are associated with distances in the other matrix, and whether that association is positive or negative. The null hypothesis that would be posited with this test is that similarities among watersheds in the past have no relationship to similarities among watersheds currently.

Another way to assess whether there was a significant effect of time on similarities/distances among communities within a watershed is to run a blocked Multi-response Permutation Procedure (MRPP). A blocked MRPP analysis with pairs of watersheds as the blocks, and past versus modern watersheds as the treatments was conducted on the entire dataset of 5 past and 5 modern watersheds combined. This is a nonparametric analysis that randomly reassigns the sample units (in this case, species incidences) among the watersheds within the treatments in order to identify whether there is a significant difference among the two groups of watersheds related to time (the distance matrix is calculated based on Euclidian distance). The signifiance value is calculated as the ratio of the number of randomizations that produced a greater difference between past and present watersheds than the actual difference divided by the total number of randomizations performed. 1000 randomizations were performed for this test.

Ordination was recommended by Rahel (2002) in his comprehensive review of the causes and consequences of homogenization as a valid way of assessing homogenization among aquatic biotas. Basically, ordination involves the projection of the watershed assemblages onto a reduced set of axes that are scaled to match gradients in community composition in the data. Nonmetric Multidimensional Scaling (NMS) and Detrended Correspondence Analysis (DCA) ordinations were performed on a matrix containing both the past and modern watersheds and the aggregated species list from both sets of watersheds (a matrix of 10 watersheds by 121 species). These ordinations provided an additional multivariate approach with which to assess the similarity among species assemblages in different watersheds, and gave a visual depiction of the similarities among watersheds. The NMS analysis is generally recommended over the DCA because it is more stable, and does not make as many assumptions about the structure of the data (Mccune and Grace 2002). However, the DCA ordination provides axes that are scaled to species turnover, providing the interpreter of the graph with a seemingly more direct relationship between the ordination space and beta diversity (or similarity). Therefore, I conducted both of these ordinations using PC-ORD. PC-ORD uses NMS methods defined by Mather (1976) and Kruskal (1964), and DCA methods defined by Hill and Gauch (1980).

The ordinations provide a launching pad from which to examine the amount of homogenization that has occurred among specific pairs of watersheds that were located closest to each other in species space. This will also indicate which watersheds should have more attention paid to how their communities have changed compositionally.

Finally, the significance of the difference between the similarity of a pair of watersheds in the past and that of a pair of watersheds from the modern dataset can be calculated using the MRPP analysis described above without assigning watersheds to blocks. This can be done using the actual sample by species matrix of the pairs of watersheds, and randomly reassigning the samples to different watersheds.

Results

Completeness ratios and alpha diversity within watersheds

The use of the completeness ratio allowed an assessment of how much of the true stream fish diversity in a watershed was characterized by the samples from the past and modern datasets. This was important to gage in order to make the most accurate beta similarity estimation possible. Table 1 contains the completeness ratios and species richness values for all watersheds with significant areas located within the Kansas border. The Middle Arkansas, Republican, Missouri-Nishnabotna and Arkansas-Keystone watersheds had completeness ratios less than 0.76 (76%) based on the past species data, indicating that at least 24% of the diversity (richness) of these communities was not included in the database. In order to make the most accurate assessment of homogenization possible, only those watersheds with a completeness ratio of over 80% were included in the analysis. These better-characterized watersheds were: the Gasconade-Osage, the Kansas, the Upper Cimmaron, the Smoky Hill and the Neosho-Virdigris (these watersheds are highlighted in Table 1. The best-characterized watershed across both past and modern databases was the Kansas watershed (Completeness ratio = 0.88 and 0.96 respectively using past and modern data), and the worst was the Republican (Completeness ratio = 0.41 and 0.83 respectively using past and modern data).

After the completeness ratios were calculated, the reduction in watersheds used in the analysis reduced the past data to 514 samples (2,424 individuals) and the modern dataset to 46 samples (57,879 individuals). Originally, the past dataset contained 120 species from streams in Kansas, while the modern dataset contained 90 species. After the data reduction, species richness was 115 for the five past Kansas watersheds, and 85 for the five modern Kansas watersheds used in the analysis. The aggregated species lists are provided in appendix Table A. Highlighted species in one dataset are not present in the other dataset.

In the past dataset, the watersheds with the highest and lowest alpha diversity (species richness) respectively were the Neosho Virdigris (91 species) and the Upper Cimmaron (13 species). In the modern dataset, the highest diversity was also found in the Neosho Virdigris (70 species), while the lowest was found in the Smoky Hill watershed (16 species) (Table 1).

To envision the diversity present at different scales, Table 2 shows the mean alpha diversity, beta diversity (spatial turnover of species among watersheds) and gamma diversity of fish faunas in the study area. The modern fish data revealed lower average alpha diversity per watershed, lower beta diversity and lower gamma diversity than the past fish data. Table 2 includes calculations of the change over time in these diversity measures. The most striking difference is that the modern agency dataset (post-1988) contains 30 fewer species than the past museum dataset (pre-1958).

Coarse-grain assessment of the amount of homogenization among watershed fish faunas in Kansas

Beta similarities (based on the Sorensen index) for the 10 pairs of watersheds are shown in Table 3, which also shows whether there was an increase (indicating homogenization) or decrease in similarity among pairs of watersheds over time. As mentioned above, beta similarity is a measure of the complementarity (the opposite of species turnover) of faunas across two different habitats. In this case, the watershed is the habitat. The mean beta similarities for the five Kansas watersheds in the past and modern time-frames are shown in Table 4 along with the differences between the mean beta similarities for these two time periods. Table 4 reveals that there was an 8.2% increase in mean similarity among these watershed faunas between the past (pre-1958) and modern (post 1988) time-frames according to the Sorensen similarity index, and a 6.6% increase in mean faunal similarity according to the Jaccard index. A paired one-tailed t-test was conducted to evaluate the significance of these differences between the past and present mean beta-similarities. The differences were significant ($p<0.03$) using both the Jaccard ($t = -2.3$) and the Sorensen ($t = -2.25$) indices.

For an additional indication of how much homogenization has occurred with time, the similarity of specific pairs of watersheds in the past was compared to their modern similarity, and the number of increases and decreases in similarity among pairs of watersheds was recorded (see Table 3). Of the 10 pairs of watersheds, 3 pairs of watersheds became less similar to each other (their Sorensen similarities decreased) and 7 pairs of watersheds became more similar to each other (their Sorensen similarities increased). The same result was found using the Jaccard index. The particular pairs of watersheds that became more or less similar to each other will be discussed below.

In order to look at whether homogenization has masked the influence of past patterns in watershed similarity on modern among-watershed similarities, a Mantel test (statistical comparison of similarity matrices) was done. This test basically evaluates whether the pattern of similarity among pairs of watersheds in the past is related to the similarity patterns seen among pairs of watersheds today. The standardized Mantel statistic (basically a correlation coefficient) was $r=0.7699$ (range from -1 to 1) for the association between past and present similarities among watersheds and was significant ($p=0.05$) according to the Monte Carlo randomization test. This indicates that there was a significant positive association between the similarities present among watersheds in the past, and the pattern of modern watershed similarities.

As stated previously, another way to assess whether there was a significant effect of time on similarities/distances among communities within a watershed is to run a blocked Multi-response Permutation Procedure (MRPP) on the entire combined dataset of five past and five modern watersheds. Essentially, this is a randomization test that retains the structure of the treatments (past or modern), and assesses whether the same differences between past and modern watersheds could be found by chance. The blocked MRPP analysis revealed that the overall difference between the pairs of past and modern watersheds was significant ($p=0.02$) and strong ($t=-2.69$). The strength of the effect of the treatment (time) is described by the t-statistic. The more negative the t-statistic is, the stronger the treatment effect.

Ordination of watershed fish faunas to visualize homogenization

Detrended Correspondence Analysis (DCA) and Nonmetric Multidimensional scaling (NMS) were conducted to give a visual depiction of the similarity among watersheds. These ordinations were done with watersheds from both the past and present, which were plotted on the same graph to look at similarity between past watersheds, between modern watersheds, and to compare past and modern biotas within the same watershed.

The NMS ordination plot can be seen in Figure 2. For the NMS ordination, the Sorensen similarity (or distance) index and PCORD default settings were used. The program conducted 40 runs with real data. The dimensionality of the dataset was assessed by visually inspecting the NMS Scree plot, from which it was apparent that two dimensions were the appropriate number to use in order to reduce stress to a manageable level in the analysis. The stress reported with the final ordination solution was 2.83, which is an acceptable value that produces an interpretable ordination plot (Mccune and Grace 2002). A Monte Carlo test (randomization test) was then performed to assess the probability that a similar final stress for the NMS ordination could have been obtained by chance (p=0.0196). The final ordination solution was obtained after 50 iterations, and the stability of the solution was assessed by visually inspecting a plot of stress to iteration number (stress hit a stable plateau at about 25 iterations, indicating a stable solution). To assess the effectiveness of the ordination (i.e., the amount of variance in the data that was represented by the two axes), the correlation between the Sorensen distances among the original watershed communities and the distances among points within the ordination space was calculated. This calculation revealed that the cumulative proportion of the variance represented by both axes was 0.955. However, the two axes were somewhat related (orthogonality=51%).

The NMS plot (Figure 2) shows a distinct separation between the watershed faunas in the past and the present along one dimension or axis (axis 2). This separation is apparent along axis 2 for all of the watersheds except for the Upper Cimarron, which had past and modern faunas that separated out along axis 1. The Kansas and Upper Cimarron watershed faunas seem to have changed the most over time according to this plot. It is also apparent that some of the pairs of watersheds that were more distinct have become more similar in the present. Those pairs with faunas that have become more similar according to this analysis include: the Smoky Hill and Upper Cimarron; the Gasconade-Osage and Kansas; the Kansas and Smoky Hill; the Upper Cimarron and Smoky Hill; the Kansas and Upper Cimarron; and the Neosho Virdigris and Upper Cimarron watersheds. The spread of the past watershed data points is also much broader in both dimensions of the ordination than that of the modern data. The NMS ordination was performed using the Jaccard similarity measure as well, and produced similar results (plot not shown).

For the Detrended Correspondence Analysis (DCA), two ordination axes were interpreted (see ordination plot in Fig. D). To assess the effectiveness of the ordination (i.e., the amount of variance in the data that was represented by the two axes), the correlation between the Euclidian distances among the original watershed communities and the Euclidian distances among points within the ordination space was calculated. From this, it was determined that the cumulative proportion of the variance represented by both axes was 0.435. Additional output from PCORD revealed that the two axes were weakly related (orthogonality=80%).

The past and modern watersheds distinctly separated out into two groups along axis two in the DCA plot (Fig. D). This trend was not noted for the Upper Cimarron watershed, which instead had past and modern faunas that separated along axis one. Also, the Smoky Hill watershed did not follow this trend due to the presence of its past fauna in the same region of axis two as the modern watershed faunas. In contrast to the NMS plot, the DCA plot also revealed that the Neosho-Virdigris watershed fauna changed the most over time. The Smoky Hill watershed fauna seems to have changed very little over time compared to the other watersheds, which was also not indicated in the NMS plot.

A closer look at homogenization among specific pairs of watersheds

The ordinations of the watersheds in the above analyses and the beta similarity values from Table 3 indicated which pairs of watershed biotas had grown more similar to (or more distant from) each other with time, and therefore should be examined more closely. As mentioned above, Table 3 revealed that the fish faunas within three pairs of watersheds became less similar to each other (their Sorensen similarities decreased), but the fish faunas within the other seven pairs of watersheds became more similar to each other (their Sorensen similarities increased). The pairs of watersheds that had a decrease in similarity or an increase in beta diversity were: the Neosho-Virdigris and Gasconade-Osage; Smoky Hill and Gasconade-Osage; and the Neosho-Virdigris and Kansas watersheds. Table 3 also shows the percent change over time in similarity among pairs of watersheds. Of the seven watershed pairs that showed an increase in similarity, four of these pairs showed an increase in betasimilarity of over 20%, and all of these pairs of watersheds included the Upper Cimarron as part of the pair. Therefore, the Upper Cimarron became more similar to all of the other watersheds in the analysis between the two time frames assessed here. The highest increase in similarity among watersheds was seen in the Upper Cimarron and Kansas watershed pair (117% increase). The watershed pair that changed the least was the Smoky-Hill and Kansas watershed pair (increase in faunal similarity of 0.711%).

The Neosho-Virdigris and Gasconade-Osage watersheds had the most complementary, or similar, fish faunas in the past (S.I. = 0.689, indicating that these faunas were 68.9% similar) (See Table 3). Based on the modern data, the Kansas and Gasconade-Osage watershed faunas were the most similar (S.I. = 0.716, or 71.6% similar). The least similar watersheds were the Upper Cimarron and Neosho-Virdigris for the past data (20.2% similar) and the Smoky Hill and Neosho-Virdigris for the modern data. The Neosho-Virdigris and Gasconade-Osage watersheds were the second most similar pairing of watersheds in the modern time-frame. These relationships are corroborated in the ordination plots (Figures 2 and 3). To further characterize the faunal change among watershed pairs, the number of species shared by pairs of watersheds was calculated using both the past and modern data. Table 5 reveals that four pairs of watersheds had an increase in the number of species shared (mean = 45.6 % increase), but six watershed pairs had fewer species in common over time (mean decrease = 31% per watershed pair).

The ordination plots (Figures 2 and 3) allow an initial idea of how similar the current fauna in a watershed is to its faunal composition in the past. It is notable that some modern watershed faunas are oriented closer to other modern watershed faunas than they are to the same watershed in the past. This is particularly true for the Gasconade-Osage, Kansas and the Neosho-Virdigris watersheds. In addition, Table 6 contains the Sorensen faunal similarity values for each watershed compared to itself over time. The Neosho-Virdigris watershed fish fauna maintained the highest similarity (S.I. = 0.81, scale of 0 to 1), while the Upper Cimmaron was the most changed – had the lowest similarity (S.I. = 0.61) - between the two time periods.

However, in an analysis such as this, which directly compares faunas from the same location but from two disparate time periods, and where data are not similarly sampled, additional description is very important. Therefore, Tables 7 and 8 were constructed to display the species that were lost or gained based on the comparison of the pre-1958 museum data and the post-1988 agency reference stream data in both the

Neosho-Virdigris and Upper Cimarron watersheds; the watersheds with the highest and lowest similarity values from Table 6. The Neosho-Virdigris had a species richness of 91 in the past and 70 in the modern dataset, while the Upper Cimarron showed an increase from 13 to 20 fish species between the past and modern datasets (Table 9). Table 7 reveals that 23 species were lost and two were gained in the Neosho Virdigris watershed. The Upper Cimarron, on the opposite end of the spectrum, gained nine species and only lost two (see Table 8). The specific characteristics of those species lost or gained in these two watersheds will be discussed below.

<u>The change in faunal composition of the entire five-watershed area over time</u>

The faunal lists from the five best-characterized watersheds were aggregated, and a comparison of the past and modern aggregated lists was made in order to look at the change in community composition that occurred at the coarser scale (see Appendix Table A for the species lists). The species accumulation curves for both the past and modern data indicated that, at the scale of the state, the curve had nearly reached a complete plateau (the saturation point) (data not shown). This means that the sampling effort had nearly attained all possible species in the area of interest. Therefore, this may be considered as a more robust comparison of the change in faunas over time than the finer-scale watershed work. This trend of better accuracy at the coarse scale was found in other studies that employed incidence-based collection data (e.g., Soberon et al. 2000). As mentioned above, the past assemblage from these five watersheds contained more species (115) than the modern assemblage of fish species (85), with a total loss of diversity or richness of 30 species (see Table 4). The Sorensen similarity between the two faunas from different time periods was 0.81, while the Jaccard similarity was 0.68 ($p<.000001$ for both indices based on the MRPP randomization test using samples), indicating a minimum of a 19% change in the stream fauna of the five-watershed area over time. The species lists between the two time periods were compared, and the species lost or gained were listed in Table 10. Overall, the five waterseheds lost 35 species, and gained five species. Four out of the five species that were gained were either introduced to this region through stocking or bait buckets (e.g., the red river shiner, *Notropis bairdi*). Of the 35 species that were lost over time, 28 were either rare, declining or officially listed as threatened, endangered, or in need of conservation federally or in Kansas (Cross and Collins 1995 - also see comments section of Table 10).

Discussion

Completeness ratios and alpha diversity within watersheds

The calculation of the completeness ratios based on estimates of the true number of species present in each watershed allowed the identification of the best-characterized watershed faunas for this analysis of homogenization among watersheds in Kansas. These best-characterized watersheds were: the Gasconade-

Osage, the Neosho-Virdigris, the Smoky Hill, the Upper Cimarron and the Kansas. Through its applicability to calculating the completeness ratio, the ICE estimator (Colwell 1997) was a useful tool in trying to clean or reduce the data so that the five most fully characterized watersheds could be compared over time. The ICE estimator could also be useful in future studies attempting to compare historic, non-replicated biological data with modern agency data. Beyond its utility in identifying the most fully-characterized faunas with which to assess homogenization, the assessment of the completeness ratio for each watershed (see Table 1) revealed a lack of sampling in some regions historically. For example, the completeness ratio for the past Republican watershed fauna was 0.41, indicating that potentially only 41% of the species in the watershed were accounted for in the samples included in the database. This information is important to acknowledge when trying to reconstruct an accurate picture of past faunas in these watersheds to address future research questions.

In addition to the completeness ratios, Table 1 also reveals that, even with so many more individuals, the agency data had fewer species (30 fewer species than the modern data). This could either be due to less extensive sampling, to a decrease in some species population numbers, or to a complete loss of some species in a watershed. After closer examination of the species list for the past data, this discrepancy is likely due to the fact that many of the species that have been lost between the past and modern time periods are rare or in need of protection either regionally or federally (see Table 10), so these species were easier to miss in routine sampling and have most likely declined in number since the past data were collected rather than completely disappeared.

The modern fish data revealed lower average alpha diversity per watershed, lower beta diversity and, in particular, lower gamma diversity than the past fish data (Table 2). Gamma diversity decreased more sharply than the other measures of diversity. This increase in the detectability of homogenization at a coarser scale is somewhat expected, because of the paradox of biotic homogenization, wherein a loss of fine-scale diversity may not be as apparent (due to the addition of introduced species), even though an overall loss in regional (gamma) or global diversity has occurred (Rahel 2000).

Coarse-grain assessment of the amount of homogenization among watershed fish faunas in Kansas

The mean beta similarity comparison (Table 4) indicated that biotic homogenization has occurred among watershed fish faunas in Kansas. Specifically, the Sorensen index indicated a mean increase in beta similarity or complementarity among watersheds included in the analysis of 8.2%. Also, Table 3 revealed that the majority of watershed pairs (seven out of ten pairs) had an increase in faunal similaritiy with time, with the exceptions being the Kansas and Gasconade-Osage, the Neosho-Verdigris and Gasconade-Osage and the Neosho-Verdigris and Kansas watershed pairs. From this information, it can be stated that watersheds in this five-watershed area in Kansas generally did partition more distinct faunal regions before the effects of major dam building, channelization and dewatering of streams. Therefore, it is likely that the physical boundaries to species dispersal represented by these watersheds had more impact on structuring fish communities in the past than they do today.

The Mantel test (statistical comparison of similarity matrices) indicated that there was a significant positive association between the similarities among watershed faunas in the past, and the pattern of modern faunal similarities. That is to say, the more similar a pair of watersheds was in the past, the more similar they are currently. Essentially, the pattern of species turnover in the past seems to still have an impact on the pattern of species turnover we see today. Since these historic patterns are still detectable in modern species distributions, this is a sign that the physical boundaries to dispersal (one type of isolating pressure) represented by the watershed did indeed shape historic fish community patterns, and that this type of boundary to dispersal is still influencing fish community patterns today (albeit to a lesser extent than in the past). Indeed, at a coarser scale than the watersheds analyzed here (4-digit HUCs), Hawkes (1986) found that major patterns in fish distributions in Kansas corresponded with the historically influential Mississippi and Missouri drainages more closely than with ecological regions. It can be concluded from the Mantel test results that biotic homogenization has not completely masked the influence of historical patterns in watershed faunal similarity on modern among-watershed similarity.

The blocked Multiresponse Permutation Procedure (MRPP) results indicated a significant effect of time on faunal similarity among watersheds that was not random, and could not be reproduced by substituting sites into watersheds from the opposite time-frame and rerunning the similarity analysis. This analysis essentially provides corroborative evidence of the significance of the difference between the mean beta similarity calculations over time (Table 4).

Ordination of watershed fish faunas to visualize homogenization

Ordination was recommended by Rahel (2002) in his comprehensive review of the causes and consequences of homogenization as a valid way of assessing homogenization among aquatic biotas. Both of the ordination techniques employed here revealed a distinct separation between past and modern watersheds along one axis, but not the other, indicating that one of the axes (axis two in both ordination plots – Figures 2 and 3) corresponds distinctly with the effect of time on faunal similarity among the five Kansas watersheds. The Upper Cimarron watershed did not follow this trend in either of the analyses – its past and modern fauna separated out along the opposite axis. This may have been because the Upper Cimmaron watershed gained the most species (proportionate to its past species list) of any of the watersheds in the analysis, and also because the majority of these new species are recent introductions (i.e., they have expanded their ranges due to human activities - e.g., fish stocking) in the last 50 years (see Table 8). The fact that all of the other past and modern watershed faunas separated along the other axis indicates that the change in their species composition over time may have been due more to the loss of species than a significant gain in regionally or globally exotic species. Likely, an ordination plot of the watersheds with data from modern perturbed streams added to the modern reference stream species lists used here would reveal a separation between past and present faunas more like that of the Upper Cimarron, because this addition would add more introduced species or species that are expanding their ranges.

From the NMS plot, it is also apparent that some of the pairs of watersheds that were more distinct have become more similar in the present (Figure 2). Those pairs with faunas that have become more similar according to this analysis include: the Smoky Hill and Upper Cimarron; the Gasconade-Osage and Kansas; the Kansas and Smoky Hill; the Upper Cimarron and Smoky Hill; the Kansas and Upper Cimarron; and the Neosho Virdigris and Upper Cimarron watersheds. The Upper Cimarron has become more similar to all of the other watersheds included in the analysis, likely again due to its gain in fish species that have spread due to human activities. Another indication that homogenization has occurred across the Kansas watersheds included in this analysis is the broader spread of the past watersheds in both dimensions of the NMS ordination (Figure 2) than the spread of the modern watershed faunas.

A closer look at homogenization among specific pairs of watersheds

The ordinations and the similarity indices calculated for specific pairs of watersheds helped to identify which portions of the study area may have been most effected or relatively unaffected by homogenizing influences.

From the ordination plots and Table 3, the pairs of watersheds that had a decrease in similarity or an increase in beta diversity were: the Neosho-Verdigris and Gasconade-Osage; Smoky Hill and Gasconade-Osage; and the Neosho-Virdigris and Kansas watersheds (see Table 3 and the DCA ordination plot – Figure 3). The decrease in similarity among the Smoky Hill and Gasconade-Osage watersheds was not supported by either of the ordination plots. Two of the watersheds are geographically adjacent to each other, but the Smoky Hill and Gasconade-Osage are not. The Smoky-Hill and Gasconade-Osage watersheds showed the biggest decrease in similarity (decrease of 6.8% according to the Sorensen index). The reason for this decrease in similarity among the Gasconade-Osage paired with the Neosho-Virdigris and paired with the Smoky Hill watersheds could be due to the fact that the Gasconade-Osage seems to have maintained proportionally more of its faunal diversity (see table 9) while the Neosho-Verdigris and the Smoky Hill watersheds have had more sizable drops in their species richness. In a similar vein, a likely explanation for the loss in similarity between the Kansas and Neosho-Verdigris watershed pair is that the Kansas watershed had a severe loss in diversity between the two time periods (from 67 to 39 species), whereas the loss of richness in the Neosho-Verdigris watershed was not nearly so severe (from 91 to 70 species).

The Upper Cimarron became more similar to all of the other watersheds in the analysis between the two time frames assessed here. Out of the seven pairs of watersheds in Table 3 that experienced an increase in faunal similarity over time, the four pairs that included the Upper Cimarron showed the greatest increase in similarity (above 20%). From this information from table 3, the ordination plots, and the fact that the Upper Cimarron gained species between the two time periods (see Table 9), it is apparent that this gain in similarity is largely because the Upper Cimarron fauna has changed more (become more similar to the other watersheds) rather than because the other watershed faunas have become more like the Upper Cimarron. Specifically, the change in the faunal composition of the Upper Cimarron is mostly due to a gain in species from nearby regions or truly exotic introductions (see Table 8).

Based on the geography of these watersheds, the Upper Cimarron fauna would not be expected to become so similar to these other faunas because it is geographically separated from all the other watersheds in this study by another watershed (the Middle Arkansas watershed – see Figure 1), and geographic distance should be one of the isolating influences on fish communities that would prevent such a dramatic increase in faunal similarity from occurring. The likely explanation for this occurrence is that a combination of major impoundment building and dewatering of streams in western Kansas combined with stocking of bait and sportfish have selected for the success of these newcomers, while endangering the few members of the naturally depauperate fauna that was originally there. This habitat alteration and the introduction of new species seems to have overridden the isolating pressure of geographic distance that should have encouraged maintenance of a distinct fish fauna within the Upper Cimarron. Indeed, Duncan and Lockwood (2001) contend that the ability of human disturbances such as habitat alteration and land-use change to mute important isolating influences on species is the most important mechanism for biotic homogenization.

The watershed pair that changed the least according to the similarity index was the Smoky-Hill and Kansas watershed pair (increase in faunal similarity of 0.711%). The moderately low complementarity of these two watershed faunas (see Table 3) was maintained and did not decrease even as both of the watersheds lost species between the past and modern time-frames (Table 9), indicating that both watersheds had changed in similar ways.

The fact that the number of species that two watersheds shared decreased for 6 out of the 10 watershed pairs by an average of 31% (see Table 5) indicates there is more species turnover among these watersheds than there was in the past. This is in contrast to the increased homogenization among pairs of watersheds based on the beta similarity comparison. However, after considering the loss in alpha diversity in all wateshеds indicated in Table 9, and the large proportion of those lost species that are considered vulnerable to regional extinction or global extinction, it seems that the decrease in shared species is likely due to differential loss of those more vulnerable species. Obviously, a loss in species that is not consistent across watersheds coupled with very little gain in species in each watershed as shown in Table 9 will cause the number of species that are shared to go down due to the differential impoverization of watershed faunas. Essentially, faunas are losing different species, which causes lower diversity within a watershed, but leads to fewer species being shared across these watersheds.

The four pairs of watersheds that showed an increase in species shared were expectedly the watershed pairs that contained the Upper Cimarron watershed. This information provides further evidence that the Upper Cimarron fauna has become markedly more similar to the other watersheds in the study, and has been more severely impacted by the combined homogenizing forces of habitat alteration and species introductions than other watersheds in the study.

The change in a watershed's fauna over time

The ordination plots (Figures 2 and 3) revealed that the modern Gasconade-Osage, Kansas and the Neosho-Virdigris watersheds are oriented closer to other modern watershed faunas than they are to their own past faunas. Of these watersheds, The Neosho-Virdigris watershed fish fauna maintained the highest similarity between its past and modern faunas according to the Sorensen index (S.I. = 0.81, scale of 0 to 1) (Table 6). Since the Neoshos-Verdigris fauna has changed the least over time according to the similarity analysis, it is likely that the other watersheds have become more similar to the Neosho-Verdigris fauna instead of it becoming more similar to them. However, the Neosho-Verdigris lost many species (see Table 9), which likely also contributed to the increase in similarity between this watershed and the others included in the analysis.

Also from Table 6, the Upper Cimmaron was the most changed – had the lowest similarity (S.I. = 0.61) - between the two time periods. This was expected, as the Upper Cimarron fauna was revealed to be much more similar to all other watersheds in the analysis currently than it was in the past (see Table 3). Also, this large change in the Upper Cimarron watershed fauna adds more evidence that the Upper Cimarron has become more similar to the other watersheds (likely by a gain in regionally adjacent species that are enhanced by human intervention) rather than the other watersheds becoming more similar to the Upper Cimarron (as stated above). However, in an analysis such as this, which directly compares faunas from the same location but from two disparate time periods, and where data are not similarly sampled, additional description is very important.

Therefore, examination of the actual species list (a look at who is actually there) is important rather than exclusively depending on ordination or similarity indices to help us understand what has happened to the actual communities in the watersheds. The Neosho-Virdigris had a species richness of 91 in the past and 70 in the modern dataset, while the Upper Cimarron showed an increase from 13 to 20 fish species between the past and modern datasets (Table 9). A comparison of the species lost or gained in these two watersheds (the watersheds with the highest and lowest similarity values from Table 6) should give an indication of how the communities have changed in these watersheds, and the reasons behind these changes, and should help us to identify possible mechanisms behind homogenization throughout the rest of the study area. Tables 7 and 8 display the species that were lost or gained in both the Neosho-Virdigris and Upper Cimarron watersheds over time. Table 7 reveals that 2 species were gained and 23 were lost in the Neosho Virdigris watershed. Both species that were gained are known to be stocked, and one is associated with marine systems as well as fresh (the inland silverside). Of the 23 species that were lost, 19 were identified as rare in Kansas, in need of conservation, threatened, or endangered (Cross and Collins 1995 and Page and Burr 1991). The Upper Cimarron, on the opposite end of the spectrum, gained nine species and only lost two (see Table 8). Seven out of the nine species that the Upper Cimarron gained have expanded their range within Kansas due to regional stocking (e.g., bluegill, *Lepomis macrochirus*), or are exotic (outside the Midwest) introductions, or have successfully expanded their range likely due to the increase in impoundments (e.g., the yellow bullhead, *Ameirus natalis*) (Cross and Collins 1995). The two species that the Upper Cimarron lost based on this comparison are both either endangered or in need of conservation (e.g., the Arkansas river shiner).

From the information above, it seems that the Upper Cimarron exemplifies the classic paradox of biotic homogenization described by Rahel (2000) in which homogenization causes an increase in diversity locally (i.e., within the watershed) due to an increase in exotic or generalist species from outside of the region, but an eventual decline in total global diversity due to the disappearance of endemics such as the Arkansas River shiner.

The kind of descriptive species lists shown in Tables 7 and 8 are especially valuable in the comparison of the change in a watershed’s fauna over time, because this kind of comparison involves a direct similarity calculation between two very differently sampled faunas (the qualitatively sampled fauna and the quantitatively sampled fauna). The comparison of beta similarities among pairs of faunas within a single time period did not involve this kind of direct comparison, and therefore is a more robust analysis.

The change in faunal composition of the entire five-watershed area over time

A comparison of the past and modern lists of all the species from all five Kansas watersheds was made in order to identify species that were lost or gained throughout the entire study area, and to understand how much the collective regional fauna has changed. As mentioned above, this may be considered as a more robust comparison of the change in faunas over time than the finer-scale watershed analysis, because the species accumulation curves indicated a proportionally much more complete characterization of the faunal composition at that scale.

The Sorensen similarity between the two faunas from different time periods was 0.81. This was equal to the highest similarity found between past and modern faunas for individual watersheds (the same similarity was found for the Neosho-Verdigris watershed). This high value may add validity to using the finer watershed scale to identify changes in faunal composition over time, because lower similarity values between the two time periods (i.e., larger changes in species composition) were detectable at that scale. Likely, the same similarity value was found in both the entire study area comparison and the Neosho-Verdigris watershed comparison, because that watershed includes most of the species contained in the five-watershed study area (90 out of the 115 species in the past and 70 out of the 85 species in the present).

The past assemblage from these five watersheds contained more species (115) than the modern assemblage of fish species (85), with a total loss of diversity or richness of 30 species (see Table 4). Overall, the five waterseheds lost 35 species, and gained five species (see Table 10). Four out of the five species that were gained were either introduced to this region through stocking or bait buckets (e.g., the red river shiner, *Notropis bairdi*). Of the 35 species that were lost over time, 28 were either rare, declining or officially listed as threatened, endangered, or in need of conservation federally or in Kansas (Cross and Collins 1995).

Why are so many species absent from the modern dataset?

There are several possible reasons for the absence of such a large number of species in the modern data set compared to the faunal diversity of the past. The possible explanations for this loss in species include: a lack or error in sampling of the region; the actual extirpation of these species from the area; or the decline of these species to such an extent that the likelihood of finding them in even a very large number of samples is extremely rare. It is likely that all three of these possibilities have combined to decrease the number of species observed in both the past and modern datasets. In particular, it seems that a significant contention of species that were lost over time in the region analysed here were particularly associated with backwaters and overflow pools along streams and rivers (e.g., *Hybognathus nuchalis*). The loss of these types of species in the modern database is likely due to the fact that channelization and modification of stream habitats have removed much of this habitat. An alternative explanation, however, could be that modern agency sampling crews do not generally target overflow pools or backwaters for routine sampling, and therefore may be missing the set of species that favor this kind of habitat.

Another issue to consider related to the loss of so many species is the exclusive use of reference streams to represent the modern fauna in these five watersheds in Kansas. Since 28 out of the 35 species that were lost were identified as vulnerable to regional or global extinction, it is more likely that we would find those fish in reference streams, which have been identified by agency and biological experts as least disturbed and most representative of the types of stream systems in the region. Therefore, it seems the choice of modern stream data was skewed toward maintaining as much fish diversity as possible per watershed and over the entire study area.

If the maintenance of fish diversity over time is more likely in reference streams, then it is puzzling why the reference streams are lacking so many vulnerable species. One must acknowledge that sampling within each stream is not exhaustive, and therefore many species may be missed. However, sampling should be representative of the variety of habitat types present in a stream reach (Plafkin et al. 1989, Paulsen et al. 1991, and Barbour et al. 1999). If managers, conservationists and researchers are identifying reference streams as benchmarks and habitats to conserve, perhaps a reevaluation is needed as to which reference streams we are choosing to represent the most desirable habitat, water quality, and biological communities that we want to maintain in a region. In short, perhaps the streams that contain these vulnerable species are being missed by our designations of reference streams. Another possibility is that stream crews avoid sampling a stream that is known to house a vulnerable species. However, from working with REMAP stream crews, I have been informed that they do sample these streams, and if they catch any endangered or threatened fish that they will measure it and throw it back. Of course, lack of taxonomic expertise can also lead to misidentification of species. For example, these same crew members recounted that since they do not have taxonomic experts in the field with them, they often will only identifiy a fish that resembles a threatened or endangered fish to genus before throwing it back.

Alternatively, the fact that these vulnerable species were not found in the reference streams also indicates the potential that some of these species have been extirpated from the region, or have declined such that they are almost impossible to find, even with the exhaustive sampling that modern agencies have undertaken (e.g., the USEPA's Regional Environmental Monitoring and Assessment Program - REMAP). In that case, we may be in the midst of a serious collapse in fish diversity that will allow a greater likelihood of invasion and establishment of exotic species even in our reference streams.

Of course, adding perturbed or non-reference sites to the modern analysis would likely allow a closer characterization of the actual contemporary richness of communities in Kansas. However, the exclusive use of reference streams provides for a more conservative estimate of the amount of homogenization that has occurred among fish communities because of the decreased likelihood that exotics are present in those streams.

Mechanisms for the homogenization of stream fish faunas among watersheds in Kansas

Because this study examined reference streams in modern times rather than a mixture of perturbed and reference streams, the homogenizing role of regional extirpations was highlighted rather than the effect of invasion by regional or exotic species. With the exception of the Upper Cimarron, reference watershed faunas have lost more vulnerable species than gained exotic species or species that are expanding their range from adjacent regions due to human activities. In this analysis, the driver of homogenization seems to be the differential loss of vulnerable species in certain watersheds, which then cause those watersheds to have fewer shared species. This differential loss in vulnerable species is supported by the calculations of vulnerable species lost per watershed in Table 9, and seems to be the cause for the increase in the number of shared species between six out of ten watershed pairs over time. Therefore, this analysis indicates that modern reference stream faunas are in the process of losing species, but not all of them are completely gone from the region as a whole – they have only disappeared from discreet portions (watersheds) of the region. Eventually, these species will be completely gone, and a loss in global diversity and regional diversity of historically present species will occur.

Other literature sources (e.g., Cross and Collins 1995) indicate that the vulnerable species that were identified as lost in this analysis are still maintaining populations in small portions of the study area. However, the fact that these species did not appear in the reference stream database indicates that these species have a great likelihood of regional or global extinction within decades, and their lack of abundance as indicated by this absence from reference streams means they do not contribute significantly to the ecological diversity in watersheds.

The conclusion that homogenization among most Kansas watershed fish faunas is likely being driven mostly by a loss of native species rather than an equal combination of introductions and species loss contrasts with the paradox of homogenization described by Rahel (2000) in which both homogenizing forces seem to play strong roles. In Rahel's scenario, native species are declining but have not disappeared. At the same time, local or alpha diversity is increasing due to invasion by exotic species, thereby masking this intermediate stage of homogenization. In four out of the five watersheds analyzed here, however, there was a very small gain in species between the past and modern time periods (between 2 and 9 species per watershed - see Table 9). This indicates that the reference streams in Kansas have not been severely invaded by exotic or range-expanding species. However, the loss in species found in these watersheds decreases competition in even these most pristine systems and allows for the increased likelihood of invasion by exotic species. Therefore, it seems that these reference streams are experiencing the process of homogenization in a different way from the scenario described by Rahel (2000). The reference streams in this study are in the process of losing their vulnerable species at different rates, which will lower alpha diversity, but will potentially maintain or increase the beta diversity among watersheds above what would be expected in the midst of species loss. This may have caused estimates of homogenization based on betasimilaritiy or beta diversity to be lower compared to areas that have had an influx of invasive species such as the Upper Cimarron watershed in this analysis, which exemplifies that paradox of homogenization scenario.

The impact of biotic homogenization of fish communities on classification strength results from Chapters one and two

One of the initial reasons for conducting this assessment of homogenization was to assess whether translocation and regional extirpations of species due to human activities could have muddied the ability of the previous two studies (Chapters one and two) to detect correspondence between patterns in reference stream fish communities and regional stream classification approaches such as watersheds and ecoregions. Homogenization (likely via loss of species) was found to occur among watersheds in Kansas, which suggests that this phenomenon has had an effect on the types of communities found in different regions within a regional classification approach, and a subsequent effect on the classification strength calculations (at least in Kansas). However, the amount of coarse-scale homogenization among Kansas watershed faunas revealed by this study (an 8.2% increase in beta similarity among watersheds) does not indicate an overly large homogenizing affect on the communities. Therefore, homogenization likely played a small role in masking the correspondence between changes in stream communities and regional stream classification approaches. Future work with past and modern data from all four states (Kansas, Missouri, Nebraska and Iowa) included in the classification strength analyses may reveal a stronger effect of homogenization on stream communities – especially with regard to the impact of invasive species.

Conclusions

Biotic homogenization (an increase in faunal similarity) among watershed fish faunas in Kansas has occurred since the start of the major building of impoundments, channelization and dewatering of streams by humans in the 1950's and 1960's. However, this homogenization was not found to be extremely high (mean of 8.2% increase in beta similarity or complementarity among five 4-digit HUCs or watersheds).

The calculation of homogenization represents the minimum homogenization that could have occurred among these watersheds, because of the use of reference stream fish to represent the modern faunas. These reference streams were used in this analysis, instead of a combination of reference and non-reference streams, because they provided the most conservative test of whether homogenization has occurred among the five watersheds due to the decreased likelihood that these streams contain invasive species.

The analysis of similarity among watersheds also revealed that the watershed was a more influential boundary to species dispersal prior to major human modifications to stream habitats.

The watershed that seemed most affected by the dual homogenizing forces of invasion and regional extinction was the Upper Cimarron, which lost two species that are vulnerable to regional extinction, but gained in alpha diversity over time due to the introduction of exotic species or of species that were expanding their ranges due to human activities.

The overall loss in species found in most watershed faunas except for the Upper Cimarron indicated that the five Kansas watersheds studied here may be experiencing a stronger homogenizing impact from local or regional extirpations than a gain in invasive species. The loss in alpha (watershed) diversity coupled with a decrease in beta diversity (or an increase in beta similarity) does not fit with the homogenization paradox described by Rahel (2000) in his state to state comparisons of homogenization among fish faunas.

Homogenization among fish communities has likely decreased the correspondence between fish community patterns and regional stream classification boundaries found with the first two chapters of this dissertation. However, the impact of homogenization was probably not large enough to have changed the results of the first two studies significantly.

This study is unique in that an analysis of biotic homogenization among fish communities at a regional scale has not been conducted for the state of Kansas, or any portions of the Midwest. Further, this initial assessment should be helpful to conservationists, managers and researchers in understanding the change that has occurred in our watershed faunas over time. In particular, because the assessment only included reference streams for the modern data, this study has provided an initial assessment of how different our reference faunas in each watershed are from our historic watershed fish faunas. These results will help the research community to understand more clearly how different the reference streams they have identified are from truly undisturbed conditions. This is an important caveat to add to any discussion of stream restoration, habitat protection, or species protection.

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TABLES AND FIGURES FOR CHAPTER THREE

	Observed		Estimated					
Watershed	Past # spp	Mod # spp	Past # spp	Mod # spp	Past Completeness Ratio	Modern Completeness Ratio	Past shannon div. index	Mod shannon div. index
ARK-KEY	39	45	51	52	0.76	0.87	3.50	2.53
GASC-OS	55	42	58	46	0.94	0.91	3.62	2.96
KS-wshed	67	39	76	40	0.88	0.96	3.69	1.94
MID-ARK	39	36	53	44	0.74	0.81	3.31	1.93
NEO-VIR	91	70	105	82	0.87	0.86	4.09	2.91
REPUB	25	30	62	36	0.41	0.83	2.94	1.63
SMO-HILL	24	16	28	20	0.85	0.81	2.35	1.33
UP-CIM	13	20	14	22	0.94	0.89	2.35	2.02
KS-state	120	90	132	104	0.91	0.87	4.21	2.75

Table 1. Species richness, Shannon diversity and the completeness ratio for Kansas watersheds and the state of Kansas calculated from the past and modern databases. The modern database comes from state agencies (quantitatively sampled). The past dataset comes from the University of Kansas' Natural History Museum collection (not quantitative samples). The estimated species richness was calculated using the incidence coverage estimation (ICE) algorithm available in the EstimateS software package (Colwell 2005). The completeness ratio is calculated as the ratio of the observed over estimated species richness after Soberon et al. (2000). Shaded watersheds have a completeness ratio of over 0.81 using both past and modern data, indicating that over 81% of the diversity in the watershed has been accounted for in the databases.

Time-frame	Alpha	Beta	Gamma
Past	50	0.553	115
Modern	37	0.471	85
Change over time	-9	-0.082	-30
% Change over time	-17.70%	-14.80%	-26.09%

Table 2. Diversity of stream fish in five Kansas watersheds over time. Alpha diversity is the average number of species per watershed. Betadiversity was also averaged, and is a measure of species turnover between two different watersheds (calculated as 1-Sorensen similarity). Gamma diversity is the total number of species across all five watersheds in the analysis.

Watershed Pair	Past beta similarities	Modern beta similarities	% change in similarity over time	Increase or decrease in Sorensen Similarity
K-G	0.672	0.716	6.53	+
N-G	0.689	0.679	-1.48	-
S-G	0.481	0.448	-6.81	-
U-G	0.235	0.484	105.65	+
N-K	0.577	0.569	-1.37	-
S-K	0.505	0.509	0.71	+
U-K	0.250	0.542	116.95	+
S-N	0.317	0.326	2.81	+
U-N	0.202	0.356	76.16	+
U-S	0.541	0.667	23.33	+

Table 3. Increasing and decreasing Sorensen betasimilarities among pairs of watersheds over time. K = Kansas, G = Gasconade-Osage, N = Neosho-Virdigris, U = Upper Cimarron, S = Smoky Hill.

	Mean Beta Similarity	
Time-Frame	Sorensen Index	Jaccard Index
Past	0.447	0.304
Modern	0.529	0.370
% Increase in Beta similarity	8.200	6.600

Table 4. Overall mean beta similarity among past and modern Kansas watersheds. Beta similarity is a measure of complementarity among watersheds, and is equal to 1-beta diversity. The increase in mean beta-similarity over time represents a coarse estimate of the amount of homogenization that has occurred across fish faunas in different watersheds over time. The increase in beta similarity for both indices was signifiant ($p<0.05$) based on paired one-tailed t-tests.

	Past	Modern		
Watershed Pair	# species shared	# species shared	Increase or decrease in number of shared species	% increase or decrease in number of shared species
K-G	41	29	-12	-29
N-G	52	38	-14	-27
S-G	19	13	-6	-32
U-G	8	15	7	88
N-K	47	31	-16	-34
S-K	23	14	-9	-39
U-K	10	16	6	60
S-N	19	14	-5	-26
U-N	11	16	5	45
U-S	10	12	2	20

Table 5. Number of species shared between pairs of watersheds in the past (pre-1958) compared to modern pairs of watersheds (post 1988). K = Kansas, G = Gasconade-Osage, N = Neosho-Verdigris, U = Upper Cimarron, S = Smoky Hill.

Watershed	Similarity of past and modern faunas
N-V	0.812
G-O	0.701
S-H	0.650
KS	0.642
U-C	0.606

Table 6. Sorensen similarity between past and modern stream fish faunas for five Kansas watersheds in the order of highest to lowest similarity. N-V = Neosho-Virdigris, G-O = Gasconade-Osage, S-H = Smoky Hill, KS=Kansas, U-C = Upper Cimarron

Species Code	Common Name	Species lost/gained over time	Comments
ANGROS	American eel	Lost	dams impeding entry to KS except in NE KS
CARAAU	Gold fish	Lost	exotic accidental introduction
CARPCY	Quillback	Lost	range expansion due to reservoirs and possible stocking
CARVEL	Highfin carpsucker	Lost	species in need of conservation
ERIMDI	Streamline chub	Lost	rare
ETHECR	Arkansas darter	Lost	threatened in KS, and endemic to Ark. river basin
ETHENI	Johnny darter	Lost	rare
ETHEPU	Stippled darter	Lost	rare
ETHGRA	Slough darter	Lost	species in need of conservation
HYBOPL	Plains minnow	Lost	species in need of conservation
HYPENI	Northern hogsucker	Lost	species in need of conservation
LUXIPI	Duskystripe shiner	Lost	rare
LUXIZO	Bleeding shiner	Lost	rare
MACRST	Silver chub	Lost	declining
MENBER	Inland silverside	Gained	ascends from ocean, or can be stocked as food fish
MICRDO	Small mouth bass	Lost	some stocking with range expansion due to impoundments
MOXOAU	Pealip Red horse	Lost	rare
MOXOCA	River redhorse	Lost	species in need of conservation
MOXODU	Black redhorse	Lost	species in need of conservation
NOCOBI	Hornyhead chub	Lost	threatened in KS
NOTRTO	Topeka shiner	Lost	endangered
NOTUIN	Margined madtom	Lost	rare
NOTUPL	Neosho madtom	Lost	threatened
PHOXER	Southern redbelly dace	Lost	declining
STIZVI	Walleye	Gained	stocked game fish, which may have been native to Kansas

Table 7. Stream fish species lost or gained over time in the Neosho-Virdigris watershed in Kansas based on a comparison of pre-1958 museum collection data compared to post-1988 agency data. Two fish species were gained and 23 were lost. Both species that were gained are known to be stocked, and one is associated with marine systems as well as fresh (inland silverside). 19 out of the 23 lost fish species are identified as rare in Kansas, in need of conservation, threatened, or endangered (Cross and Collins 1995 and Page and Burr 1991).

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Species Code	Common Name	Species lost/gained over time	Comments
AMEINA	yellow bullhead	Gained	spreading west through impoundments
CARAAU	gold fish	Gained	exotic accidental introduction
CYPRCA	common carp	Gained	exotic intentional introduction
DOROCE	gizzard shad	Gained	range expansion due to impoundments and stocking
HYBOPL	plains minnow	Lost	species in need of conservation
ICTAPU	channel catfish	Gained	range expansion due to impoundments and stocking
LEPOMA	blue gill	Gained	range expansion due to stocking
LEPOME	Longear sunfish	Gained	spreading through impoundments
MICRSA	Large mouth bass	Gained	introduced through stocking
NOTRBA	river shiner	Gained	introduced
NOTRGI	Arkansas river shiner	Lost	endangered

Table 8. Stream fish species lost or gained over time in the Upper cimmaron watershed in Kansas based on a comparison of pre-1958 museum collection data compared to post-1988 agency data. All 9 of the species gained have expanded their range within Kansas due to regional stocking (i.e., bluegill), or are exotic (outside the Midwest) introductions, or have successfully expanded their range likely due to the increase in impoundments (i.e., yellow bullhead) (Cross and Collins 1995). The 2 lost species are either endangered or in need of conservation.

Watershed	Past Diversity	Modern diversity	# species lost	# species gained	# vulnerable species lost
ARK-KEY	39	45			
GASC-OS	55	42	21	8	11
KS-wshed	67	39	32	4	17
MID-ARK	39	36			
NEO-VIR	91	70	23	2	19
REPUB	25	30			
SMO-HILL	24	16	10	2	5
UP-CIM	13	20	2	9	2
KS-state	120	90			

Table 9. Alpha diversity (by watershed), gamma diversity (entire state of Kansas), and the number of species gained or lost calculated from the past and modern databases. The modern database comes from state agencies (quantitatively sampled). The past dataset comes from a museum collection (not quantitative samples). Alpha diversity is calculated as the species richness of an individual watershed. Gamma diversity describes the collective diversity of all watersheds in the state of Kansas (the "KS-state" diversity). The term vulnerable indicates that a species is vulnerable to regional or global extinction, and has been identified as rare or in need of conservation or protection either federally or regionally.

Species Lost	Comments	Species Gained	Comments
AMEINE	Unsuccessful introduction	LEPOMI	stocked game fish
ANGROS	Rare, dams impeding entry to KS except in NE KS	MENBER	ascends from ocean, or can be stocked as food fish
CARVEL	Species in need of conservation	NOTRBA	Introduced
ERIMDI	Rare	PHOXEO	possible range expansion from North due to cooler water releases from impoundments
ESOXLU	Previously stocked game fish	STIZVI	stocked game fish, which may have been native to Kansas
ETHEPU	Rare		
ETHGRA	Species in need of conservation		
HIODAL	No population number info., but possibly declining		
HYBOAR	Threatened		
HYBOHA	Species in need of conservation		
HYBONU	Rare		
HYBOPL	Species in need of conservation		
HYPENI	Species in need of conservation		
ICTFUR	Deep river or reservoir species		
LOTLOT	Rare, impeded by upper Mo. river impoundments		
LUXIPI	Rare		
LUXIZO	Rare		
MACRAE	Endangered		
MACRGE	Threatened		
MACRME	Endangered		
MACRST	Declining		
MICRDO	Some stocking with range expansion due to Impoundments		
MOXOAU	Rare		
MOXOCA	Species in need of conservation		
MOXODU	Species in need of conservation		
NOTRBL	Species in need of conservation		
NOTRGI	Endangered		
NOTUGY	Species in need of conservation		

NOTUIN	Rare		
NOTUPL	Threatened		
PHOXER	Declining		
PLATGR	Threatened		
POLYSP	Declining		
SCAALB	Endangered		
SCAPAL	Relatively stable population		

Table 10. Fish species lost or gained across five Kansas watersheds based on a comparison of pre-1958 museum collection data and post 1988 agency reference stream data. A total of five species were gained, and 35 species lost. The following watersheds were included in the analysis: the Gasconade-Osage, the Kansas, the Neosho-Virdigris, the Upper Cimarron and the Smoky Hill.

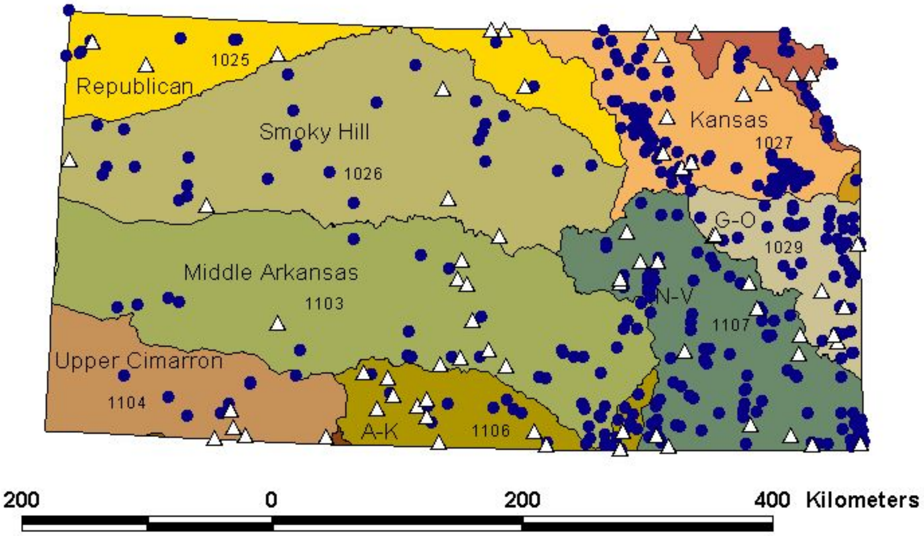
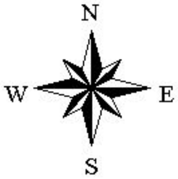


Figure 1. Stream fish sampling sites from the modern and past datasets in all nine watersheds (4-digit HUCs) in Kansas. The triangles represent the modern sites (post 1988), and the blue dots represent the past sites (pre-1958). A-K = Arkansas-Keystone watershed. N-V = Neosho-Virdigris watershed. G-O = Gasconade-Osage watershed.



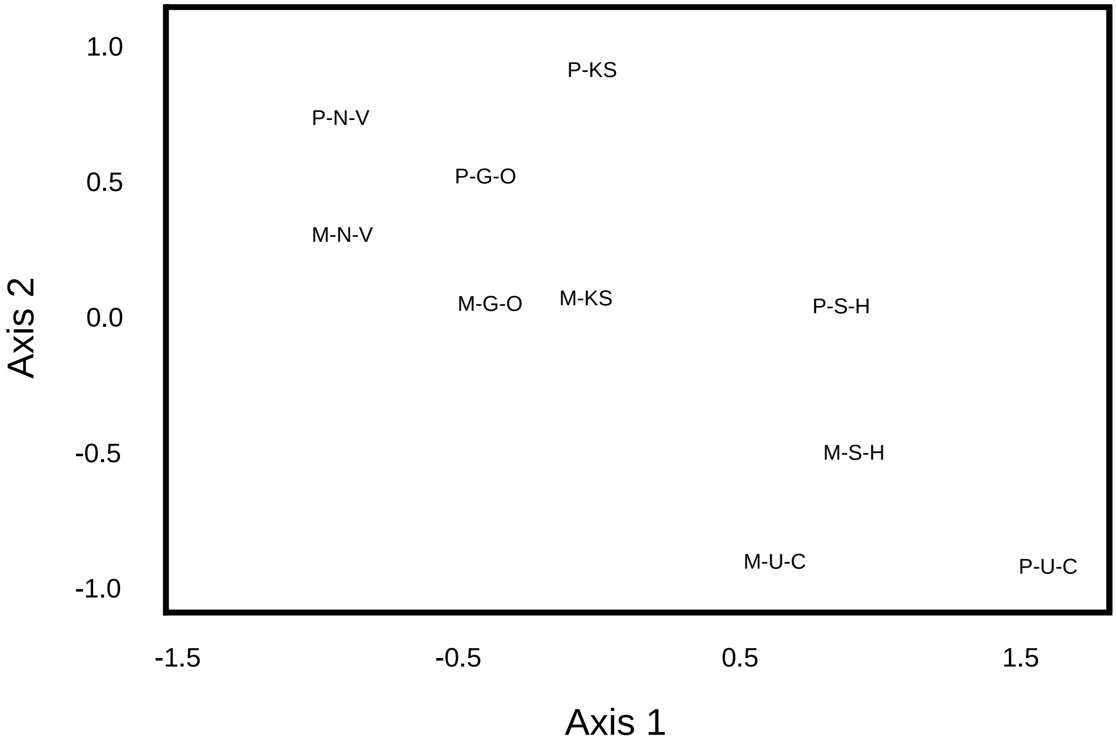


Figure 2. Nonmetric multidimensional scaling (NMS) ordination plot of past and modern watershed fish faunas on two axes. P = Past, M = Modern, KS = Kansas, G-O = Gasconade-Osage, S-H = Smoky Hill, N-V = Neosho-Virdigris and U-C = Upper Cimarron.

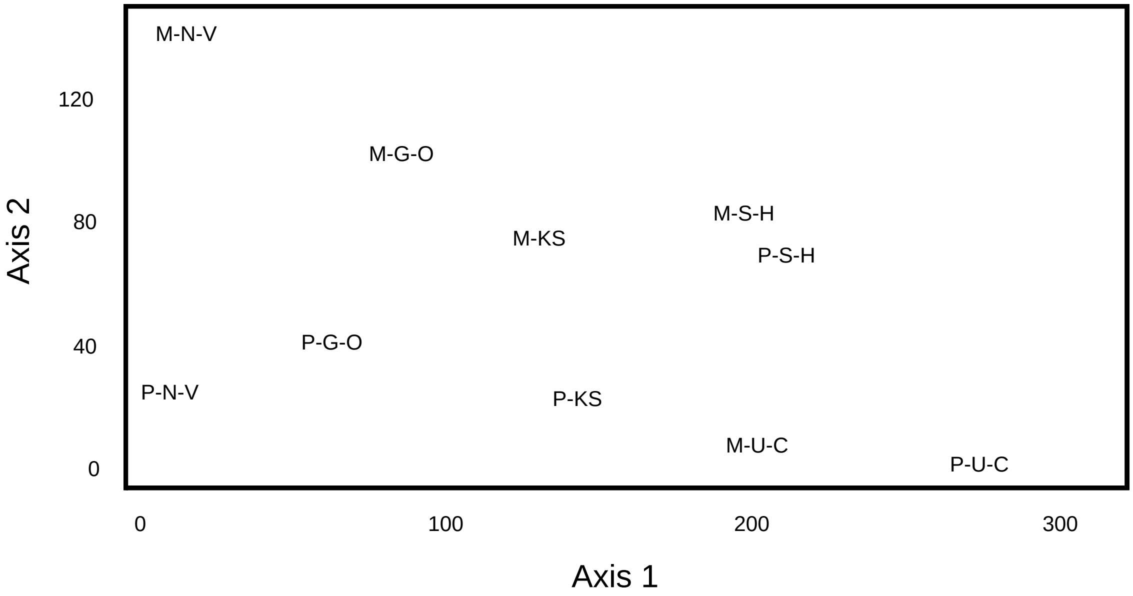


Figure 3. Detrended correspondence analysis (DCA) ordination plot of past and modern watershed fish faunas on two axes. P = Past, M = Modern, KS = Kansas, G-O = Gasconade-Osage, S-H = Smoky Hill, N-V = Neosho-Virdigris and U-C = Upper Cimarron.

Appendix for Chapter Three

Appendix Table A. Aggregated species lists for the five past and modern watersheds. Highlighted species are unique to that particular dataset, and are not present in the dataset from the other time period.

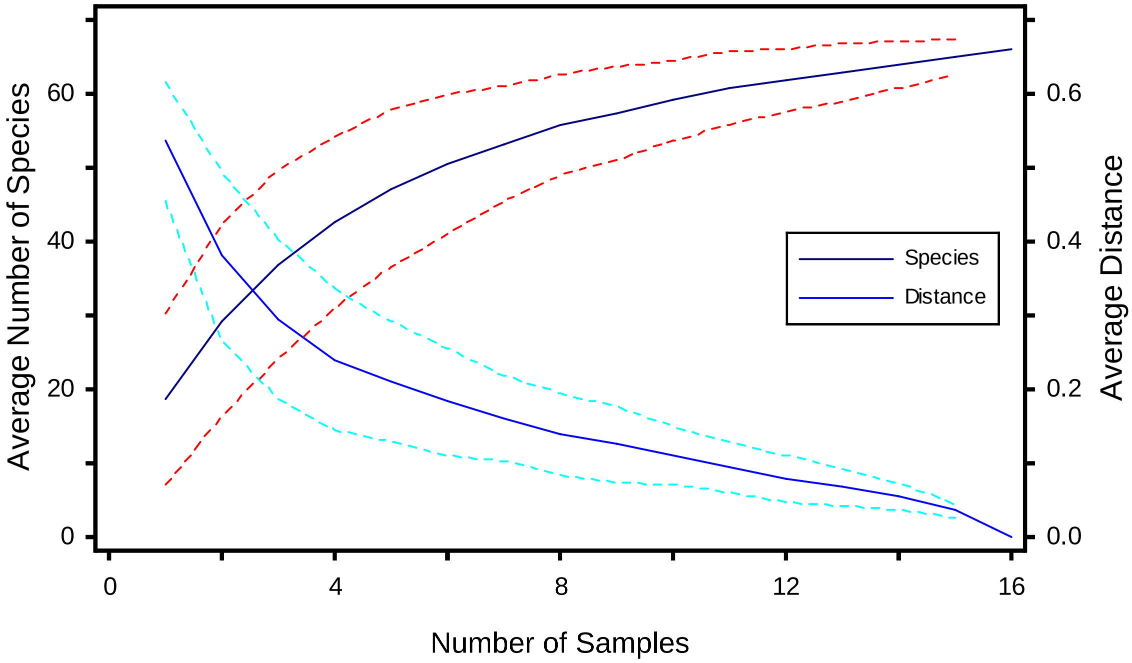
	Past	Modern
1	AMBLRU	AMBLRU
2	AMEIME	AMEIME
3	AMEINA	AMEINA
4	AMEINE	APLOGR
5	ANGROS	CAMPAN
6	APLOGR	CARAAU
7	CAMPAN	CARPCA
8	CARAAU	CARPCY
9	CARPCA	CATOCO
10	CARPCY	COTTCA
11	CARVEL	CYCELO
12	CATOCO	CYPRCA
13	COTTCA	CYPRCM
14	CYCELO	CYPRLU
15	CYPRCA	CYPRSP
16	CYPRCM	DOROCE
17	CYPRLU	ERIMXP
18	CYPRSP	ETHCHL
19	DOROCE	ETHEBL
20	ERIMDI	ETHECR
21	ERIMXP	ETHEFL
22	ESOXLU	ETHENI
23	ETHCHL	ETHESP
24	ETHEBL	ETHEST
25	ETHECR	ETHEWH
26	ETHEFL	ETHEZO
27	ETHENI	FUNDNO
28	ETHEPU	FUNDZE
29	ETHESP	GAMBAF
30	ETHEST	HYBDOR
31	ETHEWH	ICTAPU
32	ETHEZO	ICTIBU
33	ETHGRA	ICTICY
34	FUNDNO	ICTINI
35	FUNDZE	LABISI
36	GAMBAF	LEPIOS
37	HIODAL	LEPIPL
38	HYBDOR	LEPOCY
39	HYBOAR	LEPOGU
40	HYBOHA	LEPOHU

PAST
41 HYBONU
42 HYBOPL
43 HYPENI
44 ICTAPU
45 ICTFUR
46 ICTIBU
47 ICTICY
48 ICTINI
49 LABISI
50 LEPIOS
51 LEPIPL
52 LEPOCY
53 LEPOGU
54 LEPOHU
55 LEPOMA
56 LEPOME
57 LOTLOT
58 LUXICA
59 LUXICO
60 LUXIPI
61 LUXIZO
62 LYTHUM
63 MACRAE
64 MACRGE
65 MACRME
66 MACRST
67 MICRDO
68 MICRPU
69 MICRSA
70 MINYME
71 MOROCH
72 MOXOAU
73 MOXOCA
74 MOXODU
75 MOXOER
76 MOXOMA
77 NOCOAS
78 NOCOBI
79 NOTECR
80 NOTMIU
81 NOTRAT
82 NOTRBL
83 NOTRBO
84 NOTRBU
85 NOTRGI
86 NOTRNU
87 NOTRRU

MODERN
LEPOMA
LEPOME
LEPOMI
LUXICA
LUXICO
LYTHUM
MENBER
MICRPU
MICRSA
MINYME
MOROCH
MOXOER
MOXOMA
NOCOAS
NOCOBI
NOTECR
NOTMIU
NOTRAT
NOTRBA
NOTRBO
NOTRBU
NOTRNU
NOTRRU
NOTRST
NOTRTO
NOTRVO
NOTUEX
NOTUFL
NOTUNO
PERCCA
PERCCO
PERCMA
PERCPH
PERSHU
PHENMI
PHOXEO
PIMENO
PIMEPR
PIMETE
PIMEVI
POMOAN
POMONI
PYLOOL
SEMOAT
STIZVI

PAST
88 NOTRST
89 NOTRTO
90 NOTRVO
91 NOTUEX
92 NOTUFL
93 NOTUGY
94 NOTUIN
95 NOTUNO
96 NOTUPL
97 PERCCA
98 PERCCO
99 PERCMA
100 PERCPH
101 PERSHU
102 PHENMI
103 PHOXER
104 PIMENO
105 PIMEPR
106 PIMETE
107 PIMEVI
108 PLATGR
109 POLYSP
110 POMOAN
111 POMONI
112 PYLOOL
113 SCAALB
114 SCAPAL
115 SEMOAT

Appendix Figure A. The modern fish species accumulation curve for Gasconade-Osage watershed reference streams. The convex line describes the species accumulation curve.



CONCLUSIONS TO THE DISSERTATION

A major goal of modern ecology and environmental science is to identify and understand the underlying variation in natural systems, and to separate this variation from changes that are related to on-going human activities. This endeavor can be useful to scientists who are simply trying to understand natural processes more completely, but is also critical in an applied context to those who are trying to manage or conserve valuable natural resources in the midst of broad-scale anthropogenic habitat alteration. One way that scientists are trying to describe natural spatial variation in ecosystems is by creating regional classifications such as ecological regions (ecoregions) based on criteria they deem most important in shaping distinct ecosystems at a coarse scale. These classification approaches (particularly the ecoregion approach) are being applied to lotic systems in the Midwest, and can be useful tools for structuring scientific research and ecologically cognizant monitoring and management programs. However, their applicability to streams in the Midwest has not been comprehensively evaluated (Hawkins et al. 2000).

Classification approaches that may be applied to streams include: The watershed (USGS 1982 and Seaber et al. 1987); the aquatic ecological units of Maxwell et al. (1995) and the U.S. Forest Service; Strahler stream order (Strahler 1964); the ecoregions of Bailey (Bailey 1995; Cleland 1997) developed for the forest service; and the ecoregions of Omernik (Omernik 1995), which are currently being used by the USEPA. Each classification approach for streams represents a different hypothesis as to which environmental criteria are most influential to stream systems, because they emphasize different criteria in delineating distinct regions or designating stream types. Therefore, a comparison of their ability to classify distinct stream types allows one to explore the relative influence of the different criteria emphasized in these classification approaches to streams, and also allows ideas to be generated about how to improve these classification approaches for application to stream management.

This dissertation included three studies that explore large-scale patterns in stream fish communities in four states of the Midwest (Kansas, Missouri, Nebraska and Iowa) in order to inform the design of classification systems that are being applied by researchers, conservationists, and managers to streams, and in order to elucidate important mechanisms that shape stream ecosystems in this region. Stream fish community patterns were employed because they can be used as a surrogate for patterns in stream ecosystem characteristics (e.g., in-stream physical habitat and riparian condition) over the landscape.

Based on the concepts discussed above, the first two chapters included in this dissertation attempted to assess and then fine-tune the ability of the regional and non-regional classification approaches listed above to account for broad-scale variation in types of stream fish communities in Kansas, Missouri, Nebraska and Iowa. If landscape-scale patterns in fish communities corresponded best with a certain classification framework, then the criteria that are used to classify streams within that framework were likely to be very important to structuring fish communities and in shaping other ecological properties in stream systems.

In the first and second chapters, a classification strength (CS) analysis using both Sorensen (presence-absence) and Bray-Curtis (relative abundance) community similarity indices was conducted to indicate the relative ability of different classification approaches to classify stream fish communities. The classification strength calculation was based on the difference between mean within-group similarity and mean among-group similarity of fish communities in 231 reference streams. Findings from these first two chapters influenced the exploration of biotic homogenization among watershed fish faunas that was the crux of the research conducted for Chapter three. Major conclusions from these chapters are outlined below.

Major conclusions from Chapter one:

The fact that the classification scheme based on geographic distance between stream sites was the only classification system to show a superior correspondence with patterns in fish communities across both spatial scales assessed in this study (although not across both indices) indicates that there is a high degree of spatial autocorrelation in the fish communities in this part of the Midwest.

The more aquatic Maxwell et al. classification performed the most poorly of all regional classifications at the finer scale (equivalent to level III Omernik ecoregions) based on the Sørensen analysis, and not as well as the other ecoregion classifications (Bailey's and Omernik's) based on the Bray-Curtis analysis. This result may indicate that specifically aquatic criteria are not as useful as the suite of terrestrial and climate criteria assumed by the other classifications to shape regional patterns in stream ecosystems in the Midwest at this scale.

The non-regional *a priori* Strahler stream orders classified the streams most poorly. Therefore, longitudinal location of a stream in a stream network, stream size and discharge do not seem as important to landscape-scale fish community patterns within the area studied here compared to ecoregion location.

Because the Bailey and Omernik ecoregional frameworks were almost equally predictive of fish patterns in the study area, there does not seem to be an advantage to the increased emphasis placed on climate in the Bailey scheme nor land use in the Omernik scheme for predicting patterns in stream biota. Alternatively, this result could be interpreted to mean that contemporary human land use may be as important as climate in shaping stream communities.

This study also revealed that the application of the type of ecological regions studied here seemed to be more appropriate for U.S. streams in the Midwest and Oregon than for streams in the East - particularly in the Mid-Atlantic Highlands.

Based on the detailed evaluation of the species assemblages, the classification strength assessment of ecoregions may be useful for showing general trends in communities related to large scale environmental factors, or for highlighting large homogeneous intact ecosystems like the Flint Hills, but not for highlighting rare or threatened species assemblages. This is important information for those attempting to apply the ecoregions analyzed here in a conservation context.

The results suggest that physical boundaries to species dispersal may be having an impact on stream biota that is nearly as important as the suite of strictly ecological factors that are represented in the ecoregions frameworks. This finding was the influence for the work in Chapter two, in which the ecoregion frameworks stratified by HUCs were tested to see if this new hybrid classification would have stronger predictive powers for stream communities in this part of the Midwest.

Overall, the results from Chapter one indicated that the ecoregion classifications are useful – that they do include criteria that account for variation in fish community patterns - especially based on species presence/absence. However, they also indicate that there is still quite a lot of variation unaccounted for by the classifications tested here – particularly related to the realized niche of a species/assemblage as revealed by patterns in abundance. Obviously, there are aspects of the ecoregion delineation process that need to be altered to improve their applicability to streams. However, the weak performance of all the classifications leads to a question: "Has human-mediated extirpation and translocation of assemblages muddied the distinct differences in fish communities that may have been present historically among ecologically distinct regions?" This question was addressed in Chapter Three, which looked at biotic homogenization across fish communities in Kansas.

The research in Chapter one was unique in that no work has been done to compare competing classification approaches for streams in this part of the Midwest. Also, the database constructed for this analysis can be used to address other research questions regarding landscape-scale community fish ecology outside the scope of this work.

Chapter two attempted to combine the strength of the watershed and ecoregion frameworks into one by stratifying the two ecoregion frameworks (Bailey 1995and Omernik 1995) by watershed (HUC) in order to understand how physical and ecological boundaries to fish dispersal might interact to influence patterns in stream fish communities. The classification strength for this new hybrid framework was then tested using fish community patterns based on species, but also based on adult trophic and reproductive functional groups. It should be noted that this was the first multi-state cluster analysis of stream fish communities based on functional guild for this part of the United States.

Major conclusions from Chapter two:

Given the generally poor to similar performance of the ecoregion/watershed hybrid classification approaches relative to the unaltered regional stream classification approaches (except in the comparison with the watershed framework), this study does not support the use of the hybrid frameworks at the scale of this analysis in this part of the Midwest. However, given that this was the first time hybrid regions were constructed and tested on streams for this part of the Midwest, further testing of the hybrid regions, and construction of these regions at different scales, would be prudent to assess whether they can be applied as a structuring framework to conduct research, conservation, management and monitoring of streams.

Since the addition of the HUC/watershed boundaries improved the CS of the HUC framework, but did not improve the Bailey or Omernik ecoregion frameworks' classification strength, this provides some initial evidence that ecological boundaries to dispersal are more influential to fish community structure than physical boundaries to dispersal in this part of the U.S.

Both types of functional guilds corresponded poorly with hybrid regional divisions compared to the correspondence of the hybrid divisions with patterns in species. Surprisingly, the poor correspondence between functional groups and the hybrid regions was not due to the fact that types of functional guild communities do not show distinct geographic affinities. A cluster analysis revealed that there was distinct geographic clumping in three taxonomic clusters constructed from the reproductive guild community data. When projected onto a map, three regions of distinct combinations of reproductive guild communities were revealed, which seem to indicate a gradient of influential conditions that may run from the southeast to the northwest portion of the study area. The scale at which these geographic groups of similar guilds were identified indicates that broader-scale environmental processes (including climate cycles impacting regional temperature and precipitation gradients) than those associated with the intermediate scale of the hybrid framework analyzed here may be shaping patterns in reproductive guilds.

An overview of the performance of portions of the study area where multiple ecoregions are nested within a watershed or, alternatively, where multiple watersheds are nested within an ecoregion indicates that environmental factors that are associated with the ecoregion (ecological limitations to dispersal) have a greater impact on fish community structure at a coarser scale, while the physical boundaries to dispersal represented in the watershed are more influential when used to make finer-scale subdivisions within the ecoregion framework. This supports the contention of Omernik and Bailey (1997) that the watershed and ecoregion are complementary frameworks, and are best used in combination to classify streams in certain regions.

Finally, an analysis of several smaller regional divisions that shared adjacent ecoregions, shared adjacent watersheds, or were spatially segregated gave evidence that physical boundaries to dispersal represented by watersheds and ecological boundaries to dispersal represented by ecoregions do not seem to influence the distribution and structure of stream fish communities as strongly as spatial separation between communities at the scale of this analysis. This finding is consistent with the superior performance of the geographic distance classification framework in Chapter one.

The low raw classification strength values produced in the first two chapters inspired the third chapter. The first two chapters indicated that there is a large amount of variation in fish community patterns that is unexplained by any of the classifications (even the classification based on taxonomic similarity). One reason for this result could be that the non-random translocation and extirpation of species by human activities may have caused homogenization of once-regionally-distinct fish communities, which could blur the correspondence that might have been seen between fish community patterns and the classification schemes tested here. Therefore, Chapter three compared beta similarity of fish communities among watersheds in the past (pre-1958) to beta similarity of fish communities among watersheds in modern times (post 1988) to assess whether biotic homogenization of fish fauna in Kansas has occurred and to quantify that homogenization.

Major Conclusions from Chapter three:

Biotic homogenization (an increase in faunal similarity) among watershed fish faunas in Kansas has occurred since the start of the major building of impoundments, channelization and dewatering of streams by humans in the 1950's and 1960's. However, this homogenization was not found to be extremely high (mean of 8.2% increase in beta similarity or complementarity among five 4-digit HUCs or watersheds included in the analysis).

The calculation of homogenization represents the minimum homogenization that could have occurred among these watersheds, because of the use of reference stream fish to represent the modern faunas. In other words, this was a conservative test of homogenization, because these reference streams are less likely to contain exotic species.

The analysis of similarity among watersheds also revealed that the watershed was a more influential boundary to species dispersal prior to major human modifications to stream habitats.

The watershed that seemed most affected by the dual homogenizing forces of invasion and regional extinction was the Upper Cimarron, which lost two species that are vulnerable to regional extinction. But, the Upper Cimarron gained in alpha diversity over time due to the introduction of exotic species or of species that were expanding their ranges due to human activities.

The overall loss in species found in most watershed faunas except for the Upper Cimarron indicated that the five Kansas watersheds studied here may be experiencing a stronger homogenizing impact from local or regional extirpations than a gain in invasive species. The loss in alpha (watershed) diversity coupled with a decrease in beta diversity (or an increase in beta similarity) does not fit with the homogenization paradox described by Rahel (2000) in his state to state comparisons of homogenization among fish faunas.

Homogenization among fish communities has likely decreased the correspondence between fish community patterns and regional stream classification boundaries found with the first two chapters of this dissertation. However, the impact of homogenization was probably not large enough to have changed the results of the first two studies significantly.

This study is unique in that an analysis of biotic homogenization among fish communities at a regional scale has not been conducted for the state of Kansas, or any portions of the Midwest. Further, this initial assessment should be helpful to conservationists, managers and researchers in understanding the change that has occurred in our watershed faunas over time. In particular, because the assessment only included reference streams for the modern data, this study has provided an initial assessment of how different our reference faunas in each watershed are from our historic watershed fish faunas. These results will help the research community to understand more clearly how different the reference streams they have identified are from truly undisturbed conditions. This is an important caveat to add to any discussion of stream restoration, habitat protection, or species protection.

In summary, the work conducted with this dissertation, and especially the database that was painstakingly constructed for the analyses, can be useful to a broad variety of endeavors related to streams. Researchers will be able to use the results to inform the design of future studies in landscape-scale patterns in fish communities in this part of the country. In addition, this kind of information is equally important to managers and monitoring agencies that rely upon regional classifications to shape management goals and regional metrics of stream health. Finally, this work will hopefully be useful to conservation organizations (e.g., The Nature Conservancy), which are currently employing specific types of regional classifications to choose regionally representative stream ecosystems to target for restoration or conservation.

FUTURE WORK

Future research should analyze the classification strengths for ecoregions and other regional frameworks at finer scales. Omernik level IV ecoregions should be assessed for Chapter 1, and level III ecoregions stratified by 4-digit HUCs should be assessed for Chapter 2. Of course, the robustness of future analyses at the finer scale is dependent on the density of data available at that scale.

The designation of orders has been refined since the completion of this research. The use of these newly designated stream orders may produce enhanced correspondence between the non-regional stream order classification and patterns in stream fish communities.

Finally, perturbed sites could be used in the future to address the questions raised in all three chapters. The addition of perturbed sites to the database analyzed in the first two chapters would inform the scientific community of the correspondence of these regional classification frameworks with the broader range of fish communities that are represented in disturbed streams. The addition of perturbed sites to the third chapter would allow a better assessment of the combined homogenizing impact of invasive species and regional/global extinction.