AN ABSTRACT OF THE DISSERTATION OF

Valerie Kelly for the degree of Doctor of Philosophy in Fisheries Science presented on November 6, 2008.

Title: Influence of Streamflow Regime and Biotic Interactions on Fish Assemblage Structure in Rivers of the Northern Great Plains

Abstract approved:

_____

Dixon H. Landers   Hiram W. Li

This study evaluates the functional organization of stream fish assemblages in response to streamflow factors and biotic interactions across a range of spatial scale. The study area for this project includes 109 stream reaches located on tributaries to the upper Missouri River in the northern Great Plains. Fish distribution data was provided by the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Program. The analysis examined assemblage structure in terms of the distribution of ecological traits along gradients of streamflow regime, and proceeded in several phases. First, a methodology was assembled for estimating ecologically relevant metrics to describe streamflow regime where streamflow data were not available. Second, co-occurrence patterns for species and their traits were examined at two levels of spatial scale in order to evaluate the relative role of environmental filtering and competitive exclusion. Third, a structural equation analysis was conducted to examine the role of specific components of streamflow regime as constraints on the expression of fish life-history strategies within local assemblages, including an evaluation of factors across a range of scale that were associated with

flow patterns. This analysis also incorporated an aggregate measure of the potential for biotic interactions at the assemblage scale.

Results for the streamflow analysis describe distinctive regional patterns of flow regime across the study area. A clear snowmelt signature was observed for streams in the western mountains, with little variability in peak-flow magnitude or timing. These streams contrast with those in the lowlands further east, which were consistently characterized by greater variability in peak-flow timing and magnitude as well as higher probability of intermittent flow. Species co-occurrence patterns were consistent with a strong tendency for local coexistence to be mediated primarily by present or past competition, resulting in spatial segregation of species when they share similar feeding strategies. At the regional scale, a contrasting pattern was observed where species with similar life-history traits tended to cluster together. These results indicate that critical niche dimensions may be defined at several levels of scale. Furthermore, these dimensions apparently are associated with ecological processes that can oppose one another across scale. Finally, SEM results indicate that small, short-lived opportunistic species were significantly influenced by regional patterns of streamflow variability while large, long-lived periodic species responded more strongly to variability at the smaller scale of the stream network. On the other hand, species with strategies to maximize juvenile survival (i.e. equilibrium strategists) showed negligible response to flow variability at any scale. These results presumably reflect the versatility of this strategy regarding physical habitat conditions. This research demonstrates that stream fish assemblages are structured at multiple levels of spatial scale by biotic interactions as well as characteristic responses of life-history strategies to streamflow variability.

Influence of Streamflow Regime and Biotic Interactions on Fish Assemblage
Structure in Rivers of the Northern Great Plains

by

Valerie Kelly

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented November 6, 2008
Commencement June 2009

Doctor of Philosophy dissertation of Valerie Kelly

presented on November 6, 2008.

APPROVED:

_____
Co-Major Professor representing Fisheries Science

_____
Co-Major Professor representing Fisheries Science

_____
Head of the Department of Fisheries and Wildlife

_____
Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

_____
Valerie Kelly, Author

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

DEDICATION

This dissertation is dedicated to my son, Dimitri David.

Influence of streamflow regime and biotic interactions on fish assemblage structure in rivers of the northern Great Plains

General Introduction

Community ecology is dominated by several ongoing debates that are linked with one another, with the first question being whether rules apply in the organization of communities or if community structure is simply random. Some ecologists are convinced that general and predictable understanding of community organization is not possible because ecological systems are too complex and dependent on idiosyncratic local history (Lawton, 1999). On the other hand, others have proposed that our understanding of how communities are organized will be advanced by examining the distribution of species traits along environmental gradients (McGill and others, 2006). Within the trait-based perspective, a second debate concerns the relative role of abiotic and biotic processes in determining community organization. Abiotic processes can be viewed as environmental filtering processes, whereby conditions of physical habitat filter or limit the kinds of traits that co-occurring species possess (Poff, 1997). These processes tend to cluster similar species together because of the shared advantage of their characteristics in response to habitat conditions. Biotic processes include several kinds of interactions, one of the most frequently studied being competition, where species may exclude one another if they are dependent on the same resources (MacArthur and Levins, 1967). Competition tends to segregate similar species from one another when those resources are limited. A third debate is related to the occurrence of these factors across a range of scale, and especially whether local or large-scale processes dominate in community organization (Levin, 1992). Of particular interest to me is the interaction of these processes across multiple levels of scale in stream systems (Fausch and others, 2002). The research described in this dissertation addresses the issues described by these debates, focusing on the role of selected abiotic and biotic factors in structuring stream fish assemblages in the upper Missouri Basin.

Streamflow regime was a primary focus for this analysis because it represents a key component of physical habitat for stream systems that varies across a range of scale (Biggs and others, 2004). Additionally, streamflow characteristics have been found to be related to functional organization of stream communities (Ward and Stanford, 1983). Key streamflow components were examined in the context of habitat

template theory, which provides the basis for organizing the physical features of habitat along dimensions of variability (Southwood, 1977). These dimensions are associated with predictions about the ecological characteristics of species that will persist under those conditions (Southwood, 1988). As such, it represents a useful framework for evaluating species response to streamflow characteristics.

Ecological traits selected for analysis included those related to habitat and trophic associations as well as reproductive strategies. Habitat and trophic similarities imply similarities regarding utilization of resources, and thereby provide a useful perspective on the role of biotic interactions on species co-occurrence. Reproductive strategies relate to the ability of a species to persist under a range of flow disturbance conditions, and so are likely to be closely related to the role of environmental filtering on species distribution patterns.

The foundation for this analysis is the ecological database collected by the U.S. Environmental Protection Agency (EPA) as part of the Environmental Monitoring and Assessment Program (EMAP) for surface waters in the western United States. A major focus for the EMAP research strategy is to develop an approach for regional assessment of ecological conditions in rivers, with an emphasis on describing ecological system integrity within the context of anthropogenic stress (Hughes and others, 2000). The study area for this project is a subset of the larger area included in the EMAP design, comprised of tributaries to the upper Missouri River in the northern Great Plains.

The overall goal of this research was to refine understanding of the functional organization of stream fish assemblages in response to physical and biotic factors across a range of spatial scale. The first chapter develops an approach for quantifying streamflow regime in a way that is ecologically relevant for streams where streamflow data are not available. The second chapter examines co-occurrence patterns for species and their traits at two levels of spatial scale in order to evaluate the relative role of environmental filtering and biotic interactions. The third chapter describes a structural equation analysis of specific components of streamflow regime proposed as constraints on fish life-history strategies within local stream assemblages, including the evaluation of large-scale factors that are associated with flow patterns.

References

Biggs, B.J.F., V.I. Nikora, and T.H. Snelder, 2004. Linking scales of flow variability to lotic ecosystem structure and structure. River Research and Applications 21: 283-298.

Fausch, K.D., C.E. Torgersen, C.V. Baxter, and H.W. Li, 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52(6): 483-498.

Hughes, R.M., S.G. Paulsen, and J.L. Stoddard, 2000. EMAP-Surface Waters: a multiassemblage, probability survey of ecological integrity in the US.A. Hydrobiologia 422/423: 429-443.

Lawton, J.H., 1999. Are there general laws in ecology? Oikos 84: 177-192.

Levin, S.A., 1992. The problem of pattern and scale in ecology. Ecology 73: 1943-1967.

MacArthur, R. and R. Levins, 1967. The limiting similarity, convergence and divergence of coexisting species. The American Naturalist 101: 377-385.

McGill, B.J., B.J. Enquist, E. Weiher, and M. Westoby, 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21(4): 178-185.

Poff, N.L., 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of North American Benthological Society 16: 391-409.

Southwood, T.R.E., 1977. Habitat, the templet for ecological strategies? The Journal of Animal Ecology 46(2): 336-365.

- 1988. Tactics, strategies and templets. Oikos 52: 3-18.

Ward, J.V., and J.A. Stanford, 1983. The intermediate disturbance hypothesis: an explanation for biotic diversity patterns in lotic ecosystems, p. 327-356 *in* E.D. Fontaine, III and S.M. Bartell (eds.) Dynamics of lotic ecosystems. Ann Arbor Press, Ann Arbor MI.

Ecologically relevant quantification of streamflow regime in ungaged streams

Introduction

Streamflow represents a critical component of temporal variability in stream systems, and is considered to be a major organizing feature of physical habitat for aquatic biota. Streamflow characteristics integrate multiple watershed factors and are related to many structural habitat features in streams, as well as to the functional organization of stream communities (Leopold, 1994; Ward and Stanford, 1983). An ecologically relevant description of the streamflow regime is provided by the variability in streamflow from floods (e.g. which is associated with increased water velocities and corresponding substrate movement) and prolonged low-flow periods (especially intermittent or periodic zero-flow conditions) (Poff and Ward, 1989). Metrics to describe patterns of these extreme events can be determined from streamflow frequency curves, and concisely represent various components of the respective flow regime so that objective comparisons can be made among regimes for different sites.

The purpose of this paper is to describe regionalization techniques that estimate ecologically relevant streamflow metrics for ungaged sites in the upper Missouri River Basin. These metrics focus on the annual time scale, and primarily indicate the magnitude of departure from the central tendency for measures of streamflow volume and timing (Table 2.1). As such, these metrics describe relatively long-term patterns of peak and low flow regimes rather than short-term recent streamflow history or current flow conditions, and therefore provide insight into potential biological responses at the corresponding scale. For example, variation in annual streamflow magnitude is closely associated with key life cycle components in fish (Scheidegger and Bain, 1995), while timing of annual flow peaks is often an important cue for spawning (Fausch and Bestgen, 1997; Nesler and others, 1988). Additionally, streamflow variability is a key factor related to disturbance for streams and has been proposed as the dominant organizing force in stream ecology (Resh and others, 1988; Fausch and others, 2001). As a result, the ability to estimate selected components of streamflow regime for sites where no streamflow data exist provides important context for evaluating ecological conditions in streams.

Overview of approach Analysis of streamflow patterns is frequently based on annual streamflow frequency information that, in the United States, is supplied primarily by data from the U.S. Geological Survey (USGS) streamflow database. The necessary data are available only for sites where long-term gaging stations are located, however, and appropriate streamflow data are not available for most stream reaches. Regional frequency analysis provides a way to estimate the frequency distributions for a variety of peak- and low-flow metrics at ungaged sites, based on pooled data from gaged sites within a homogeneous region (Stedinger and others, 1993). In this study, an index procedure was used, whereby the regional frequency curve was scaled by a site-specific scaling factor (termed the "index flow," e.g., the mean peak or low-flow value for the site) (Hosking and Wallis, 1993). Accordingly the regional curves define the dimensionless frequency distribution for the region, from which specific quantile estimates for ungaged sites can be determined on the basis of estimated values for the index flow for those sites. Several steps are required for any regional index-flow analysis: (1) identification of homogeneous regions, (2) choice and estimation of a regional frequency distribution, and (3) estimation of the index flow.

Perhaps the most critical assumption for any index-flow procedure is that the scaled frequency distributions for all sites within the region are similar. Geographically contiguous regions have frequently been defined according to physiographic and political boundaries, but these do not often correspond to similarities in hydrologic response (Simmers, 1975). For this analysis, a "region of influence" approach was used to group sites into regions according to basin features that are observed to be associated with streamflow characteristics (Wiltshire, 1986). In this approach to regionalization, it is possible for every site to have a unique set of basins defined as its hydrologic "region" that are not necessarily spatially contiguous (Burn, 1990a, 1990b: Zrinji and Burn, 1994). These sites are selected from the correspondence between selected hydrologic and watershed characteristics as determined by canonical correlation analysis (CCA) (Ribeiro-Corea and others, 1995). CCA provides canonical scores that reflect the correlation structure between the two sets of variables for gaged sites. These scores, in turn, are used to determine the associated score on the hydrologic vector from watershed data for individual ungaged

sites where no hydrologic data are available. An ellipsoidal region around each hydrologic score is then identified with a defined level of confidence based on a chi-squared distribution. This region contains the basins that compose the corresponding so-called hydrologic neighborhood or site-specific region for the target site.

Another important assumption of regional streamflow analysis is that watersheds with similar attributes, especially regarding climate, topography, vegetation, soils, and geology, will exhibit similar streamflow patterns (Cunnane, 1988).   The extent of human activity and water use in the basin is also an important factor, especially related to low-flow conditions, although it has not often been included in regional analysis because of the difficulty in quantifying these effects (Smakhtin, 2001). For this analysis, data quantifying the extent and type of human alteration of the streamflow regime (including upstream storage behind dams and water withdrawals) were included in the watershed characterization to improve the identification of appropriate regions. These metrics were derived from the National Inventory of Dams database and State water resource agencies. They describe the maximum volumes of water that can be stored or withdrawn from streams and ground water within each watershed. As a result, these metrics are indices of *potential* water pressure from human activity, rather than precise descriptions of actual water use.

After identifying the appropriate hydrologic region for each site, the next step was to select an appropriate frequency distribution to describe the regional frequency curves. Because of the focus on extreme events, the generalized extreme value distribution (GEV), based on probability-weighted moments (PWM), was selected for this analysis (Greenwood and others, 1979; Landwehr and Matalas, 1979; Hosking and others, 1985). This procedure is flexible and easy to implement, and has proven to be especially reliable when regions are not homogeneous (Lettenmaier and others, 1987). Additionally, the index flow PWM/GEV approach, based on hydrologic regions determined by canonical correlation analysis, was found to give the best results in an inter-comparison study of different procedures for rivers in Canada (GREHYS, 1996a, 1996b). The final step was the estimation of the index flows for ungaged sites by regression against appropriate watershed and climatic attributes.

Study area The inspiration and foundation for this analysis was the set of ungaged sites, which were selected as part of the Environmental Monitoring and Assessment Program (EMAP) of the U.S. Environmental Protection Agency. A major focus for the EMAP research strategy is to develop an approach for regional assessment of ecological conditions in streams and rivers across the western United States (Hughes and others, 2000), most of which are ungaged. The study area is a subset of the larger area included in the EMAP design, and is comprised of tributaries to the upper Missouri River in the northern Great Plains (Figure 2. 1).

Methods

Ungaged site selection As part of the EMAP program, the ungaged sample sites were selected according to a probability design to ensure that analytical results have clear statistical inference for the larger population of waters of concern (Stevens and Olsen, 1999). Broad spatial coverage was provided by the use of a grid network for sample selection; although pre-stratification of sites by type or region was minimal in the design, sufficient numbers of sites were selected to allow post-stratification (or classification) by a variety of criteria (Hughes and others, 2000). The sites selected for this study included both small streams (operationally defined as wadeable during summer baseflow conditions) and large rivers (similarly defined as non-wadeable). The total N for ungaged sites in the upper Missouri River Basin was 247.

Streamflow data Data for annual peak and daily mean streamflow were obtained from the online USGS National Water Information System (NWISWeb; http://waterdata.usgs.gov/nwis). For the low-flow analysis, daily mean streamflow data were first subset to include data only for the summer season (June-September); the annual 7-day minimum flow was then determined for each year.

Once the data for both peak and 7-day minimum streamflow were compiled, the data were evaluated for temporal trend as defined by Kendall's tau-b ($p<0.01$). Trend analysis proceeded in an iterative process in order to maximize the period of record for subsequent analysis. First, the data for the entire record were evaluated. For gages where no significant trend was observed, the entire dataset was included in the regional analysis. For gages where a trend was observed, a subset of the data was evaluated again, limited to the period 1960-2003. For gages where no significant

trend was observed in the subset, data from this period only were included in the regional analysis. For gages where a trend was still evident, data were subset a second time to include the period 1980-2003. If no significant trend was observed, data from this period only were included in the regional analysis.

Sites were further limited so that each had a minimum of 20 years of record between 1960 and 2003. Finally, only sites with sufficient nonzero flow over the relevant period ($N \geq 5$ where 7-day low flow ≥ 0.5 cubic feet per second) were included in the low-flow analysis. Based on this screening process, the total number of suitable gages for peak-flow analysis was 301 and 283 for 7-day low-flow analysis.

Basin characteristics As part of the initial screening process, a large number of basin characteristics were obtained for each gaging station and ungaged site, including drainage area, topography, precipitation, land use, soil characteristics, dominant ecoregion, location of major dams, and water withdrawals. Definitions of basin characteristics used in the various components of this analysis are provided in Table 2.2. All basin characteristics were extracted from GIS databases using Arc Macro Language programs written for Arc/Info (Environmental Systems Research Institute, Inc., 1999). Drainage area was determined by digitizing basin boundaries using 1:24,000 USGS topographic maps. Elevation was determined from the USGS National Elevation Database (NED), with 30 meter resolution. Annual precipitation was calculated as the sum of area-weighted estimates, based on raster precipitation data for monthly average precipitation totals (1961-1990), with 2-km resolution (Daly and others, 1994). Precipitation intensity metrics for selected recurrence intervals were calculated from raster data, including both local (site-specific) and watershed-wide characteristics (USDC, 1961; NOAA, 1973). Land use characteristics were determined by areal proportion of aggregated categories defined by data from the National Land Cover Dataset (NLCD) (Vogelmann and others, 1998). Soil characteristics were described by the sum of area-weighted values for the watershed, based on data from the State Soil Geographic (STATSGO) data base (Schwartz and Alexander, 1995). Dominant ecoregions were defined by the Level III ecoregion with the largest area within the watershed (Omernik, 1987; USEPA, 2006). The location and storage behind major dams was provided by the U.S. Army Corps of Engineers

National Inventory of Dams (NID) (http://www.nicar.org/data/dams/, accessed March 2006). Characterization of human water withdrawals within watersheds was based on an inventory of active water-permit information from State water resource agencies. The focus for the water-right analysis was limited to offstream use, that is, water withdrawn or diverted from a source (either surface water or ground water). No effort was made to distinguish consumptive from non-consumptive use, or to estimate quantities of return flow.

An *a-priori* large-scale regional classification for all sites was generated from aggregated Level III ecoregions, areas previously identified and mapped as having similar physical features, climate, vegetation, and soil characteristics (Table 2.3; Figure 2.1) (Omernik, 1987). This classification was used to pre-classify sites prior to subsequent analysis because it was presumed that these large-scale regions were characterized by distinct associations of geomorphic and climatic processes determining the streamflow regime. Since these associations were further assumed to vary among the aggregated regions across the study area, the CCA component of this analysis was conducted separately for each aggregated region.

Frequency analysis As previously mentioned, frequency analysis of annual peak- and 7-day low-flow data from gaged streams was based on an index-flow procedure, using PWM estimators of the GEV distribution (Hosking and others, 1985). The GEV distribution for any random variable (x) is described by

$$F(x) = \exp\left\{-\left[1 - g(x-u)/a\right]^{1/g}\right\}, \text{ where } g \neq 0 \tag{1a}$$

$$F(x) = \exp\left\{-\exp\left[-(x-u)/a\right]\right\}, \text{ where } g = 0 \tag{1b}$$

and *u, a,* and *g* represent parameters of location, scale, and shape. For this analysis, the probability-weighted moments (M_j) for each site were first determined as

$$M_j = \frac{1}{n}\sum_{i=1}^{n}(p_i^j Q_i), \text{ for } j = 0,1,2 \tag{2}$$

where $p_i = (i-0.35)/n$ is the plotting position estimate of F(Q) and Q_i is the series of annual peak or 7-day minimum streamflow. For the peak-flow analysis, this series was ordered from lowest to highest (i.e. $Q_1 < Q_2 < \ldots < Q_n$), so that p_i represents Px(x) or the probability of an event equal to or smaller than the designated value (Haan, 2002). For the low-flow analysis, the series was ordered in reverse, from highest to

lowest, effectively turning over the frequency curve so that the limit became a lower one (Gordon and others, 1992). In this case, the plotting position (p$_i$) represents 1-Px(x), the probability of an event greater than or equal to the designated value.

Next, the PWMs for each site were normalized by their mean ($M_j = M_j / M_0$). The parameters of the GEV distribution were estimated as follows:

$$c = \frac{2M_1 - M_0}{3M_2 - M_0} - \frac{\log 2}{\log 3} \tag{3a}$$

$$g = 7.8590c + 2.9554c^2 \tag{3b}$$

$$a = \frac{(2M_1 - M_0)g}{\Gamma(1+g)(1-2^{-g})} \tag{3c}$$

$$u = M_0 + a[\Gamma(1+g) - 1]/g . \tag{3d}$$

Finally, the selected quantiles (T-year flow events) of the GEV distribution were determined by

$$Q_T^* = u + a\left\{1 - \left[-\ln\left((1-\frac{1}{T})\right)\right]^g\right\}/g \tag{4}$$

where $g \neq 0$.

In the 7-day low-flow analysis, the presence of zero flow values (≤ 0.5 cubic feet per second) was dealt with by adjustment of probabilities based on the theorem of total probability (Haan, 2002). In other words, it was assumed that all the probability was accounted for simply by the sum of the probability of flow equal to zero plus the probability of flow greater than zero. On this basis, the frequency distribution for each site was first determined for all 7-day low-flow values greater than zero. The resulting probabilities were then adjusted by the fraction of non-zero values observed in the data for that site, effectively shifting the frequency curve along the probability axis to reflect the probability of zero flow (Gordon and others, 1992).

A probability plot correlation test was conducted to test whether the sample data from each gage were drawn from the GEV distribution (Stedinger and others, 1993). This test was based upon the correlation r between the sample data, ordered as described above, and the corresponding predicted values based upon their plotting positions. Values of r close to 1 indicated a close correspondence between the data

and the theoretical distribution. For this study, a lower critical value of *r* of 0.95
($p \approx 0.10$) was selected as the cutoff for inclusion of data in the next stage of the
analysis (Stedinger and others, 1993).

Finally, hydrologic metrics were determined for each site, either directly from
the frequency curve or calculated from the time series data (Table 2.1).

Canonical correlation analysis Separately for gaged sites within each large-
scale region, canonical correlation analysis (CCA) was performed between sets of
watershed variables and sets of hydrologic metrics using SAS CANCORR (SAS,
1989). Logarithmic transformation was applied to selected variables (drainage area,
elevation, mean annual peak-flow, and 7-day low-flow magnitude) to improve
normality of distribution and linearity of relationship between variables. The
hydrologic set included essentially the same metrics for all sites: a measure of scale
(mean annual peak or 7-day low flow magnitude), a measure of timing (mean Julian
day of peak or onset of 7-day low flow), and measures of flow variability (normalized
values of peak or 7-day low flow for selected recurrence intervals). Variability in
timing (coefficient of variation of mean Julian day) was included when it did not
correlate with timing. A measure of intermittency (proportion of 7-day low flow $\leq$
0.5 cubic feet per second) was also included in the low-flow analysis.

Variables for the watershed set were selected on the basis of correlation with
non-metric multidimensional scaling (NMS) ordination of hydrologic metrics, using
the Euclidian distance measure (McCune and Mefford, 1999). Ordinations were
performed separately for peak and low-flow metrics, and separately for each large-
scale region. All data were first relativized to the maximum value to account for
differences in scale. At least 15 iterations were used for each NMS run, based on
random starting coordinates. Each analysis was repeated several times to verify that
the solution was stable, and that the configuration represented a good fit with the data.
The number of dimensions was selected by plotting a measure of fit; a Monte Carlo
randomization test (minimum of 30 iterations) was conducted to evaluate whether the
ordination axes were extracting more variability than expected by chance (p<0.05).
Axes were rotated as appropriate to improve the interpretability of the ordination.

The relationship between the ordination scores for the hydrologic metrics and the associated hydrologic and watershed characteristics was evaluated by examination of a joint plot. These plots portrayed the direction and strength of the correlation between the two sets of variables. They provided the justification for selecting non-redundant hydrologic metrics as well as watershed variables that showed the strongest linear relationship with the ordination structure of the hydrologic regime. These always included some measure of topography, (e.g. maximum or variability of elevation within the watershed), some measure of climate (e.g. various measures of precipitation intensity), and watershed scale, as measured by drainage area. Additionally, measures describing soil characteristics, watershed slope, land cover, and water diversions were important for some components of the analysis.

The frequency analysis was limited to the first two canonical correlations, which were always significant ($p \leq 0.001$) and together accounted for essentially all the variation (cumulative proportion ranging from 0.93 to .97).

Estimation of metrics for ungaged sites Based on output from the CCA for USGS sites, scores on the first two canonical watershed variates were determined for each ungaged site using SAS SCORE (SAS, 1989). USGS gaged sites that were located near the position of each EMAP site along the watershed variate were identified by Mahalonobis distance, a multivariate distance measure that conforms to a chi-square distribution. This distribution was evaluated for canonical watershed scores (v_0) for each ungaged site along the first two canonical variates according to the following:

$$(w - \Lambda v_0)'\left(I_p - \Lambda^2\right)^{-1}\left(w - \Lambda v_0\right) \leq X_{a,p}^2 \tag{5}$$

where w is the score on the appropriate hydrologic variate for each gaged site, Λ is the eigenvalue, or squared canonical correlation between the pair of appropriate canonical variates, and I_p is the $p \times p$ identity matrix ($p=2$) (Ouarda and others, 2001). Site-specific regions for ungaged sites were defined by 90% confidence whenever possible, with a further requirement to contain at least 5 gaged sites. For some regions, it was necessary to tolerate a lower confidence in order to obtain the minimum number of sites.

Once the site-specific regions were determined, the regional PWMs were calculated as weighted averages of the PWMs for the gaged sites within each region:

$$M_{j_r} = \frac{\sum_{k=1}^{K} n_k M_j^*}{\sum_{k=1}^{K} n_k} \quad , \ j=0,1,2 \tag{6}$$

where the denominator is the total number of years of record for the region. Regional average PWMs were used to estimate the parameters of the GEV distribution based on Equation 3(a-d), and quantiles of the regional GEV distribution were calculated using regional parameter values and Equation 4. Streamflow metrics were derived directly from the regional frequency curve for each ungaged site, as described in Table 2.1. Metrics describing timing (mean and CV for Julian day) of onset of 7-day low flow were estimated from data for each site-specific region.

A modification of this procedure was used for extreme low-flow conditions at sites when "large" dams (i.e. with storage capacity > 30,000 acre feet) were located upstream. The distinction, although somewhat arbitrary, was based on the presumed capability of this volume of storage to significantly modify downstream low-flow conditions. These dams were consistently located on gaged streams, so that the selected metric was estimated for ungaged sites on these streams from the observed frequency distribution for the single gaged site rather than the theoretical distribution derived from the site-specific region.

Index flows (mean annual peak- and 7-day low-flow magnitude) were estimated by multiple regressions for those sites with no gages suitably located on the same stream. Separate regression equations were developed for each large-scale region. For sites with gages on the same stream, the index flows were calculated by drainage-area adjustment of the observed index flow for the gage (where the difference in drainage area was either within $\pm$ 33 percent or ≤ 100 miles^2).

The proportion of intermittent 7-day low flow was estimated directly from the regional frequency curve (rounded to nearest 5-year recurrence interval) for those sites with no gages nearby; where suitable gage data were available (as defined above), the proportion of intermittent flow was estimated by drainage area adjustment.

<u>Assessment of reliability</u> Any regional analysis is associated with an unavoidable level of uncertainty in the predictions, which arises in part because of the probabilistic approach. An important source of error is the regionalization process itself, especially given the assumption of sufficient similarity within regions that are defined by a small number of attributes. For this analysis, additional uncertainty occurs as a result of the confounding and dynamic nature of a range of human influence on streamflow regimes, and the challenge of quantifying that influence in a realistic and relevant way. A number of measures were taken to minimize and quantify the sources of error associated with the estimated metrics. These included the initial screening of streamflow data for gaged sites, evaluation of the probabilities associated with the definition of site-specific regions, and assessment of the errors associated with the estimation process itself by cross-validation and standard error analysis. The methods for these evaluations and their results are described in detail elsewhere (Kelly and Jett, 2006) and are not presented here.

Results

As mentioned, the first two canonical correlations were always significant ($p \leq 0.001$) for both peak and 7-day low-flow analyses in all large-scale regions and together accounted for essentially all the variation (cumulative proportion ranging from 0.93 to .97) (Table 2.4). This implies that the hydrologic variables were reliably related along the two defined dimensions to the watershed variables. Similarly, the correlation between the first canonical variate pairs was consistently high (> 0.80), while the correlation between the second canonical variate pairs was moderately high (> 0.62). These results indicate the relationships between the first pair of hydrologic and watershed variates were always strongly related, and that the second pair were at least moderately related.

From the correlations between the variables and canonical variates (not shown), the most consistent pattern observed in the peak-flow analysis was that the first canonical variate was directly associated with both mean annual peak-flow magnitude (Q_P) and drainage area. Other watershed characteristics that were associated with the first canonical variates included: elevation, precipitation intensity, and soil characteristics (water capacity, clay content, and thickness). The second

canonical variate was more varied although generally complementary to the first. In the low-flow analysis, a similar pattern of strong association of mean annual 7-day low-flow magnitude (Q_L) and drainage area with the first canonical variate was observed for all sites. Other associated watershed variables included elevation, land cover, precipitation, and water withdrawals. The second canonical variate was consistently associated with variability in low-flow magnitude ($Q100_L$) and timing (JD_LCV) for all sites.

Comparison of the metrics determined for gaged sites with those estimated for ungaged sites shows a broad overlap between the two sets within each large-scale region. Peak-flow regimes for sites within the mountains and the high xeric plateau were largely characteristic of classic snowmelt conditions, i.e. a strong seasonal signal with little inter-annual variability in magnitude of high flows. The timing metrics show that peak flow generally begins for these sites in June (Julian days 152-181) with fairly predictable timing from year to year (mostly within two to three weeks of the same date) (Figure 2. 2A and B). The inter-annual magnitude of peak flow is also relatively constrained for these sites, with the range between median values for 2-year flow and 100-year flow between 0.8 and 3.5 times the mean annual peak flow (Figure 2. 2C and D). Similar results are shown for the index of peak-flow dispersion (Q_{100}-Q_2), where median values were consistently less than 3 (Figure 2. 2E).

In contrast, lowland sites on the plains showed a much weaker seasonal signal with greater variability in magnitude of peak flow between years. Timing metrics show that peak flows generally occur a month earlier in May (Julian days 121-151), although the day frequently varies by four to six weeks (Figure 2. 2A and B). Median values for the magnitude of peak flow range between approximately 0.6 to 0.8 of the mean annual peak for 2-year flow and 4 to 7 times the mean annual peak for 100-year flow (Figure 2. 2C and D). These more variable peak-flow characteristics are also reflected in the higher values for the index of peak-flow dispersion (Figure 2. 2E).

Low-flow regimes were more similar for all regions, and generally not highly variable for either timing or flow magnitude (Figure 2. 3). The onset of low-flow conditions begins predictably late in the summer, primarily within one to three weeks of the same date (Figure 2. 3A and B). The lowland sites on the plains show only

slightly greater variability in low-flow magnitude, which generally ranges between 0.8-4 times the mean annual low flow (Figure 2. 3C-E).   The most pronounced difference between the regions is the much higher probability of intermittent flow for the plains sites (Figure 2. 3F).

The spatial distribution of estimated metrics demonstrates a clear pattern from west to east, largely reflecting the topographic gradient, for some flow features but not for all (Figure 2. 4). Timing of annual peak flow is earliest and most variable in the eastern portion of the study area (Figure 2. 4A and B). Variability in peak flow magnitude is least in the western, mountainous portion of the study area, although the largest variability is also associated with the mountainous Black Hills portion in the middle of the plains (Figure 2. 4C). Intermittent flow is clearly a major feature in small lowland streams, especially in the central region of the study area, although consistent patterns are not observed (Figure 2. 4D).

Discussion

This major purpose of this paper is to describe a procedure for estimation, or prediction, of streamflow metrics for sites where streamflow data are not available. The procedure is based on canonical correlation and frequency analysis, which are essentially descriptive techniques rather than ones suitable for testing hypotheses. CCA provided the basis for identifying watersheds for frequency analysis of data from gaged sites that were similar to ungaged sites in terms of attributes that were empirically and significantly associated with the hydrologic characteristics of interest. Because the primary emphasis of this analysis was prediction, no attempt was made to interpret the canonical variates beyond ensuring that important variables were included in the analysis.

The characterization of flow regimes based on annual metrics clearly represents a simplification of a multitude of facets of hydrologic variability that are ecologically significant. A large number of hydrologic measures across multiple temporal scales have been suggested in the literature to be biologically relevant, ranging from long-term flow patterns to characteristics of the immediate flow pulse (Poff and Ward, 1989; Puckridge and others, 1998). These include measures of magnitude and timing, such as are evaluated here, but also frequency, duration, and

rate of change (Poff and others, 1997). With the appropriate data, all these measures could be evaluated across multiple time scales, ranging from multiple years down to hours or less. Each measure can also potentially be associated with a biological response at the corresponding scale, with large-scale distribution patterns of aquatic species linked to long-term flow patterns and local stranding of juvenile fish in floodplain pools linked to flow patterns occurring at the scale of hours.

This analysis focused on estimation of metrics based on annual extremes, both of peak and low flow characteristics, not simply because of the well-developed history of frequency analysis for extreme events (Stedinger and others, 1993). These flow features, i.e. the magnitude and timing of peak and low flows, are ecologically relevant because they frequently describe critical constraints or "bottlenecks" for the completion of life histories for aquatic species. In particular, the variability in patterns of extreme events is increasingly recognized as an influential factor governing stream communities (Palmer and Poff, 1997). The composition and relative abundance of stream species can be determined largely by inter-annual patterns of variability in the intensity of high flows (Meffe and Minckley, 1987). Similarly, streams with high probability of annual intermittent flow generally are characterized by distinctive species with behavioral or physiological adaptations that allow them to persist under such harsh conditions (William and Hynes, 1977). The timing and variability in timing (or predictability) of flow events are especially important because critical life stages for many species are timed to coincide with specific flow conditions. These include fish spawning (Nesler and others, 1988), egg hatching (Naesje and others, 1995), and rearing (Seegrist and Gard, 1978).

Distinctive regional patterns of flow regime based on flow variability (i.e. characteristic streamflow features that are largely coordinated with one another) were observed in this study, similar to those described in other studies (Poff and Ward,, 1989; Puckridge and others, 1998). These patterns can be seen in the comparison of metrics for large-scale ecoregions (Figure 2. 2and Figure 2. 3) as well as in the spatial distribution of estimated metrics across the study area (Figure 2. 4). A clear snowmelt signature is shown for streams in the western mountains, with little variability in peak-flow magnitude or timing of annual peak flow (Figure 2. 4A-C). These streams

contrast with those in the lowlands further east, which are consistently characterized by greater variability in peak-flow timing and magnitude, as well as scattered streams with higher probability of intermittent flow (Figure 2. 4A-D). Because these metrics define a gradient of flow regime that is based on measures that are ecologically significant, it is likely that these streams may be ecologically distinct as well. These estimates provide the basis for evaluating the importance of flow regime to a wide range of ecological data collected for EMAP sites, as well as the means to describe flow context for any set of data collected in ungaged streams.

References

Burn, D.A., 1990a. An appraisal of the "region of influence" approach to flood frequency analysis. Hydrological Sciences 35(2): 149-165.

Burn, D.H., 1990b. Evaluation of regional flood frequency analysis with a region of influencer approach. Water Resources Research 26(10): 2257-2265.

Cunnane, C., 1988. Methods and merits of regional flood frequency analysis. Journal of Hydrology 100: 269-290.

Daly, C., R.P. Neilson, and D.L. Phillips, 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. Journal of Applied Meteorology 33: 140-158.

Fausch, K.D. and K.R. Bestgen, 1997. Ecology of fishes indigenous to the central and southwestern Great Plains. Pages 131-166 *in* Knopf and Samson (eds.) Ecology and conservation of Great Plains vertebrates. New York: Springer-Verlag.

Fausch, K.D., Y. Taniguchi, S. Nakano, G.D. Grossman, and C.R. Townsend, 2001. Flood disturbance regimes influence rainbow trout invasion success among five holarctic regions. Ecological Applications 11(5): 1438-1455.

Gordon, N.D., T.A. McMahon, and B.L. Finlayson, 1992. Stream hydrology, an introduction for ecologists. John Wiley & Sons. 526 pp.

Greenwood, J.A., J.M. Landwehr, N. N.C. Matalas, and J.R. Wallis, 1979. Probability weighted moments: definition and relation to parameters of several distributions expressible in inverse form. Water Resources Research 15(5): 1049-1054.

Haan, C.T., 2002. Statistical methods in hydrology. Iowa State Press, Ames IA. 496 pp.

Hosking, J.R.M., J.R. Wallis, and E.F. Wood, 1985. An appraisal of the regional flood frequency procedure in the UK. Hydrological Sciences 30: 85-109.

Hosking, J.R.M., and J.R. Wallis, 1993. Some statistics useful in regional frequency analysis. Water Resources Research 29(2): 271-281.

Hughes, R.M., S.G. Paulsen, and J.L. Stoddard, 2000. EMAP-Surface Waters: a multiassemblage, probability survey of ecological integrity in the U.S.A. Hydrobiologia 422/423: 429-443.

Landwehr, J.M., and N.C. Matalas, 1979. Probability weighted moments compared with some traditional techniques in estimating Gumbel parameters and quantiles. Water Resources Rsearch 15(5): 1055-1064.

Leopold, L.B., 1994. A view of the river. Harvard University Press, Cambridge MA.

Lettenmaier, D.P., J.R. Wallis, and E.F. Wood, 1987. Effect of regional heterogeneity on flood frequency estimation. Water Resources Research 23: 313-324.

Kelly, V.J. and S.M. Jett, 2006. Western Pilot Study: Ecologically relevant
    quantification of streamflow regimes in western streams. EPA/620/R-06/056.

McCune, B. and M.J. Mefford, 1999. PC-ORD. Multivariate analysis of ecological
    data, version 4. MjM Software Design, Gleneden Beach, Oregon, USA.

Meffe, G.K. and W.L. Minckley, 1987. Persistence and stability of fish and
    invertertebrate assemblages in a repeatedly disturbed Sonoran Desert stream.
    American Midland Naturalist 117: 177-191.

Naesje, T., B. Jonsson, J. Skurdal, 1995. Spring flood: a primary cue for hatching of
    river spawning Coregoninae. Canadian Journal of Fisheries and Aquatic
    Sciences 52: 2190-2196.

Nesler, T.P., R.. Muth, A.F., Wasowicz, 1988. Evidence for baseline flow spikes as
    spawning cues for Colorado squawfish in the Yampa River, Colorado.
    American Fisheries Society Symposium 5: 68-79.

NOAA (National Oceanographic and Atmospheric Administration), 1973. Atlas 2,
    Precipitation frequency atlas of the western United States. Data available on
    line (http://hdsc.nws.naoo.gov/hdsc/pfds/index.html).

Omernik, J.M., 1987. Ecoregions of the conterminous United States (map
    supplement): Annals of the Association of American Geographers 77(1): 118-
    125.

Ouarda, T.B.M.J., C. Girard, G.S. Cavadias, and B. Bobee, 2001. Regional flood
    frequency estimation with canonical correlation analysis. Journal of
    Hydrology 254: 157-173.

Palmer, M.A. and N.L. Poff, 1997. Heterogeneity in streams. Journal of the North
    American Benthological Society 16: 169-173.

Poff, N.L., and J.V. Ward, 1989. Implications of streamflow variability and
    predictability for lotic community structure: a regional analysis of streamflow
    patterns. Canadian Journal of Fisheries and Aquatic Sciences 46: 1805-1817.

Poff, N.L., J.D. Allan, M.B. Bain, J.R. Karr, K.L. Prestegaard, B.C.Richter, R.E.
    Sparks, and J.C. Stromberg, 1997. The natural flow regime. Bioscience
    47(11): 769-784.

Puckridge, J.T., F. Sheldon, K.F. Walker, and .A.J. Boulton, 1998. Flow variability
    and the ecology of large rivers. Marine and Freshwater Research 49: 55-72.

Resh, V.H., A.V. Brown, A.P. Covitch, M.E. Gurtz, H.W. Li, G.W. Minshall, S.R.
    Reice, A.L. Sheldon, H.B. Wallace, and R.C. Wissmar, 1988. The role of
    disturbance in stream ecology. Journal of the North American Benthological
    Society 7: 433-455.

SAS Institute, Inc., 1989. SAS/STAT users guide, version 6, 4th edition, volume 1 and
    2, Cary NC. 1,686 pp.

Scheidegger, K.J. and M.B. Bain, 1995. Larval fish distribution and microhabitat use
    in natural and regulated rivers. Copeia 1995: 125-135.

Schwartz, G.E. and Alexander, R.B., 1995. State soil geographic (STATSGO) data base for the conterminous United States. U.S. Geological Survey, Open-File Report 95-449.

Seegrist, D.W. and Gard, R., 1972. Effects of floods on trout in Sagehen Creek, California. Transactions of the American Fisheries Society 101: 478-482.

Simmers, I., 1975. The use of regional hydrology concepts for spatial translation of streamflow data. International Association of Hydrologic Sciences Publication 117: 109-117.

Smakhtin, V.U., 2001. Low flow hydrology: a review. Journal of Hydrology 240: 147-186.

Stedinger, J.R., R.M.Vogel, and E.Foufoula-Geoergiou, 1993. Frequency analysis of extreme events, p. 18.1-18.66 *in* D.R. Maidment (ed.) Handbook of hydrology. McGraw-Hill, Inc.

Stevens, D.L. Jr., and A.R. Olsen, 1999. Spatially restricted surveys over time for aquatic resources. Journal of agricultural, Biological, and Environmental Statistics 4(4): 415-428.

USDC (U.S. Department of Commerce), 1961. East U.S. rainfall frequency, Technical Paper No. 40, U.S. Department of Commerce, Weather Bureau.

USEPA, 2006. Level III ecoregions of the conterminous United States. URL http://www.epa.gov/wed/pages/ecoregions/level_iii.htm, accessed March 2006).

Vogelmann, J.E., T.L. Sohl, P.V. Campbell, and D.M. Shaw, 1998. Regional land cover characterization using Landsat Thematic mapper data and ancillary data sources. Environmental Monitoring and Assessment 51(1-2): 415-428.

Ward, J.V., and J.A. Stanford, 1983. The intermediate disturbance hypothesis: an explanation for biotic diversity patterns in lotic ecosystems, p. 327-356 *in* E.D. Fontaine, III and S.M. Bartell (eds.) Dynamics of lotic ecosystems. Ann Arbor Press, Ann Arbor MI.

Williams, D.D. and H.B.N. Hynes, 1977. The ecology of temporary streams. II. General remarks on temporary streams. Internationale Revue des gesampten Hydrobiologie 62: 53-61.

Wiltshire, S.E., 1986. Identification of homogeneous regions for flood frequency analysis. Journal of Hydrology 84: 287-302.

Zrinji, Z. and D.H. Burn, 1994. Flood frequency analysis for ungaged sites using a region of influence approach. Journal of Hydrology 153: 1-21.

Table 2. 1. Definitions of ecologically relevant streamflow metrics.

Streamflow metric	Measurements used to define
Peak-flow regime	
Q_P	Mean annual peak-flow magnitude
$Q2_P$	Index of bankfull flow (normalized 2-year peak flow)
$Q100_P$	Index of peak-flow variability (normalized 100-year peak flow)
D_P	Index of peak-flow dispersion ($Q100_P$-$Q2_P$)
JD_P	Peak-flow timing (mean Julian day for annual peak flow)
JD_PCV	Variability in peak-flow timing (coefficient of variation for mean Julian day)
Low-flow regime	
Q_l	Mean annual 7-day low-flow magnitude
$Q2_L$	Index of baseflow stability (normalized 7-day 2-year low flow)
$Q100_L$	Index of low-flow variability (normalized 7-day 100-year low flow)
D_L	Index of low-flow dispersion ($Q100_L$-$Q2_L$)
Pzero	Index of intermittency (percent of days/year with zero 7-day low flow)
$Q7Q10_L$	Important low-flow event (7-day 10-year low-flow magnitude)
JD_L	Low-flow timing (mean Julian day, onset of annual 7-day low flow)
JD_LCV	Variability in 7-day low-flow timing (coefficient of variation for mean Julian day)

Table 2. 2. Description of watershed characteristics used in regional frequency analysis.

Basin characteristic	Description
Drainage area	Area of watershed (square miles)
Longitude	Longitude of site (degrees)
Maximum elevation	Maximum elevation of the basin (meters)
Variability in elevation	Standard deviation for mean elevation (meters)
Watershed slope	Mean watershed slope (percent)
Percent water	Proportion of watershed covered by open water (NLCD-11) (percent)
Precipitation intensity	2-year 24-hour precipitation intensity, maximum for watershed
Peak precipitation intensity	100-year 6-hour precipitation intensity, at site
Variability in precipitation intensity	Standard deviation for watershed mean, 100-year 6-hour precipitation intensity
Soil water capacity	Available water capacity of soil (inches/inch)
Soil clay content	Clay content of soil (percent of material less than 2 mm in size)
Soil liquid limit	Liquid limit of soil (percent moisture by weight)
Soil organic material	Organic material in soil (percent by weight)
Soil thickness	Cumulative thickness of all soil layers (inches)
Total water diversion	Sum of all water permitted to be withdrawn within watershed annually (cubic feet per second)

Table 2. 3. Aggregated ecoregion classification.

Aggregated ecoregion	Level III ecoregion
Mountain (MT)	Middle Rockies
	Southern Rockies
	Canadian Rockies
Plains (PL)	High Plains
	Northwestern Glaciated Plains
	Northwestern Great Plains
	Nebraska Sand Hills
	Northern Glaciated Plains
	Western Corn Belt Plains
	Lake Agassiz Plain
Xeric high plateau (XE)	Wyoming Basin

Table 2. 4. Results from canonical correlation analysis.

Parameter	Plains		Mountains		Xeric	
Peak-flow analysis						
N for sites	204		55		48	
N for variables	10		9		9	
Canonical variate pairs	**1**	**2**	**1**	**2**	**1**	**2**
Canonical correlation	.82	.75	.95	.77	.90	.78
Overlapping variance (canonical R^2)	.68	.57	.91	.60	. 81	.61
Cumulative proportion extracted by eigenvalue	.61	.97	.83	.93	.69	.95
7-day low-flow analysis						
N for sites	182		60		63	
N for variables	9		8		9	
Canonical variate pairs	**1**	**2**	**1**	**2**	**1**	**2**
Canonical correlation	.81	.62	.87	.77	.87	.62
Overlapping variance (canonical R^2)	.65	.40	.76	.60	. 76	.38
Cumulative proportion extracted by eigenvalue	.73	.98	.81	.93	.81	.97

Figure 2. 1 Map of study area.
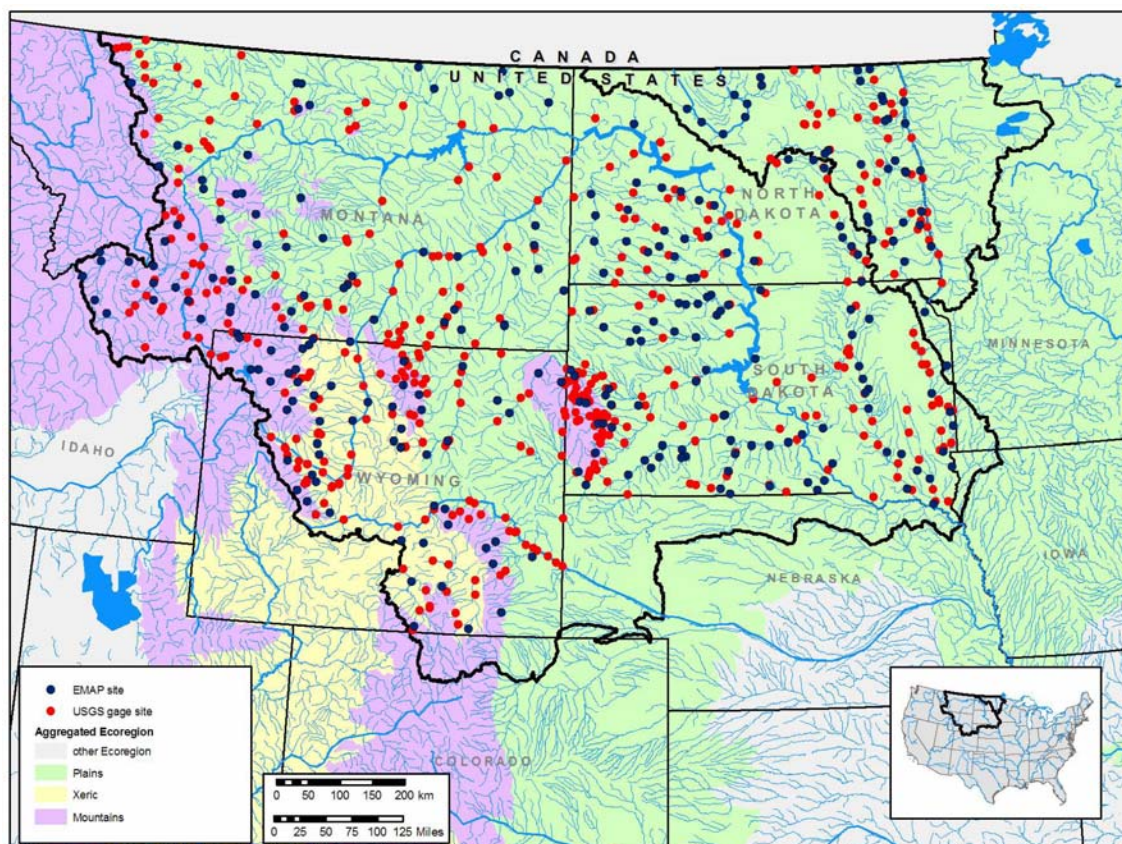
[See text for explanation of aggregated ecoregions]

Figure 2. 2. Distribution of peak-flow metrics for gaged and ungaged sites.
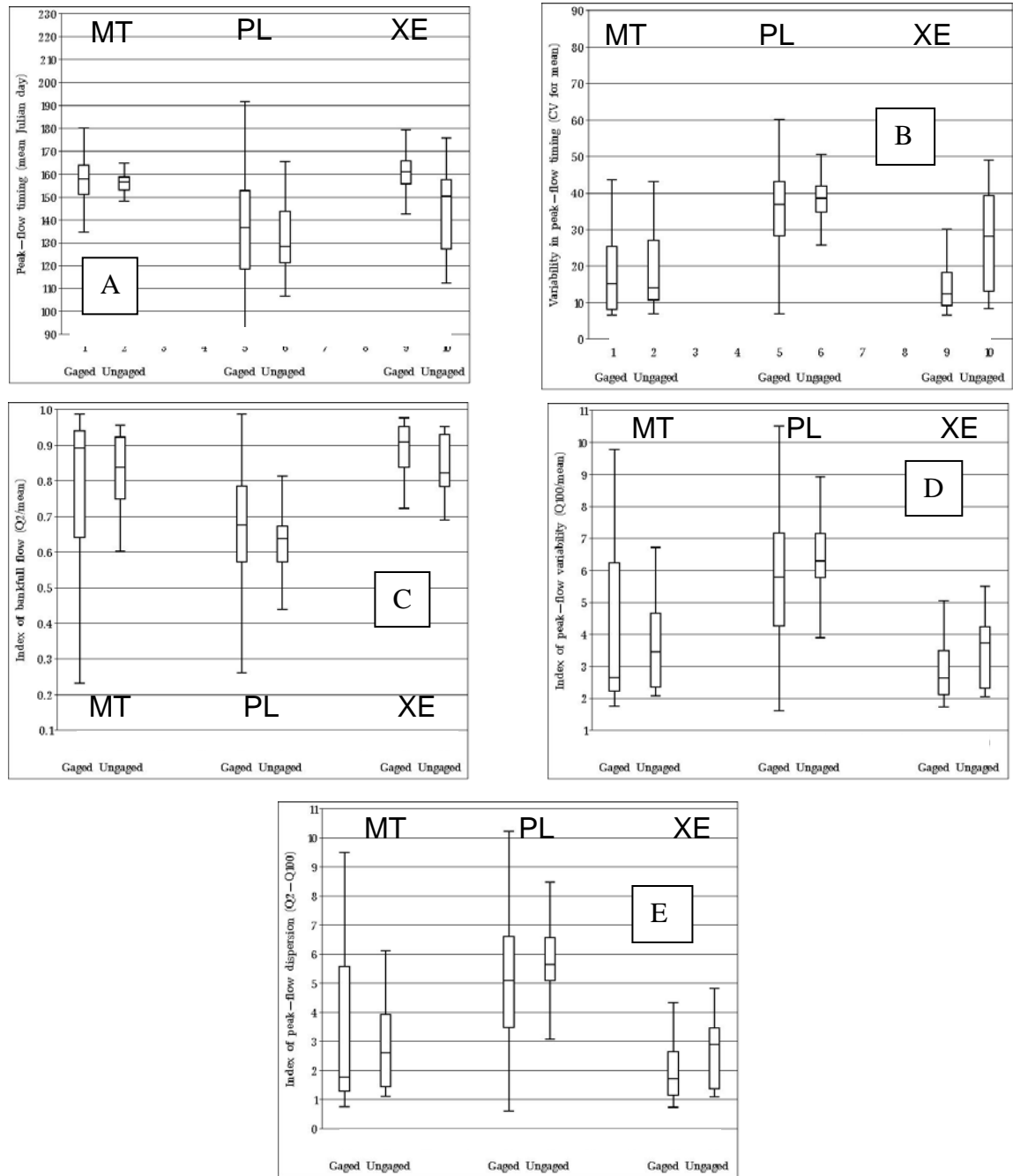
A. Mean Julian day for annual peak flow; B. Coefficient of variation for mean Julian day, annual peak flow; C. 2-year peak flow, normalized by mean annual peak flow (Q2); D. 100-year peak flow, normalized by mean annual peak flow (Q100); E. Q100-Q2.

Figure 2. 3. Distribution of 7-day low-flow metrics for gaged and ungaged sites.
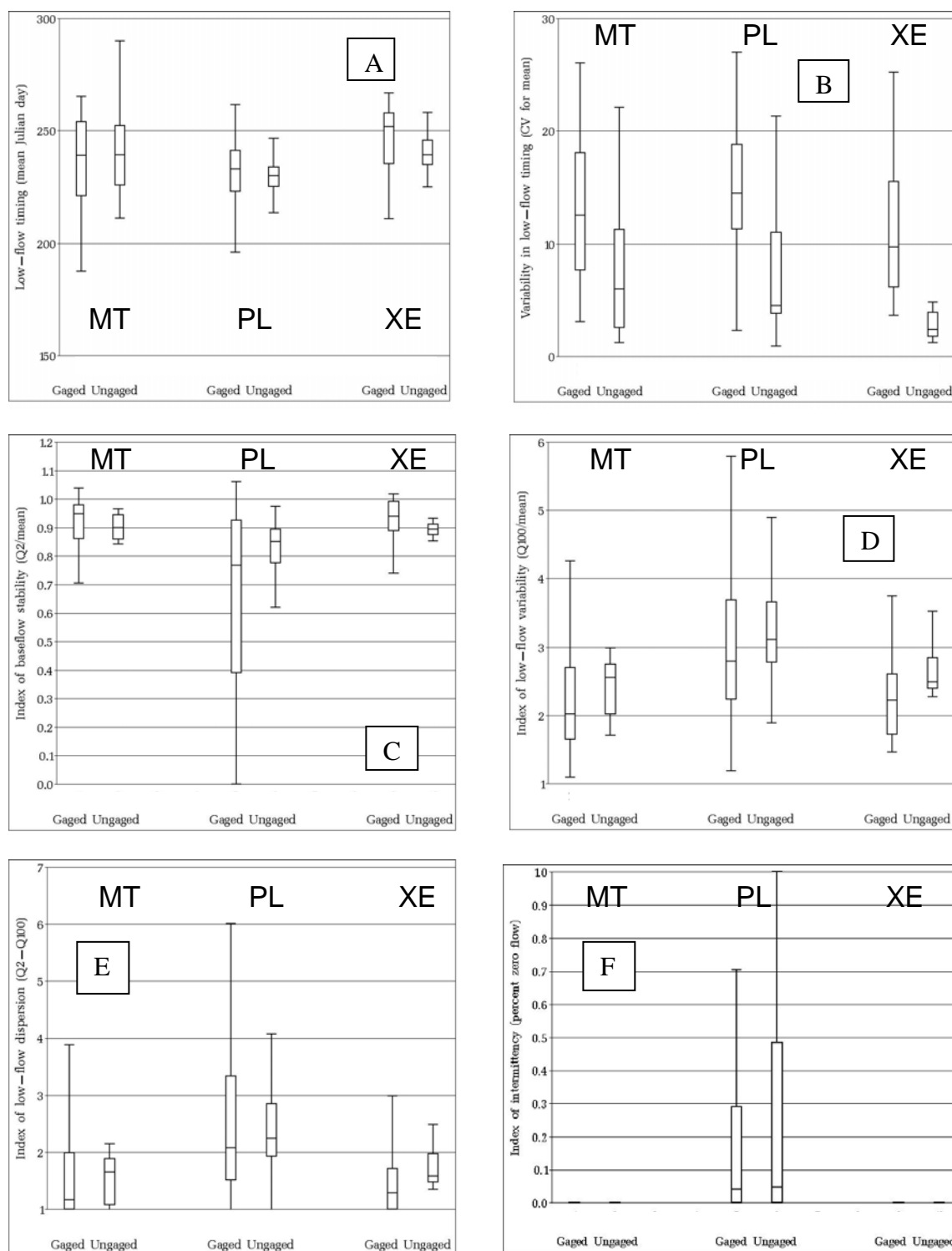
A. Mean Julian day for annual 7-day low flow; B. Coefficient of variation for mean Julian day, annual 7-day low flow; C. 2-year 7-day low flow, normalized by mean annual 7-day low flow (Q2); D. 100-year 7-day flow, normalized by mean annual 7-day low flow (Q100); E. Q100-Q2; F. probability of 7-day zero flow (< 0.5 cubic feet per second).

Figure 2. 4. Spatial distribution of selected flow metrics for ungaged sites.

Legend

timing of annual peak flow

- 🔴 April
- 🟠 May 1 - 15
- 🟢 May 15 - 31
- 🔵 June 1 - 15
- 🔵 > June 15
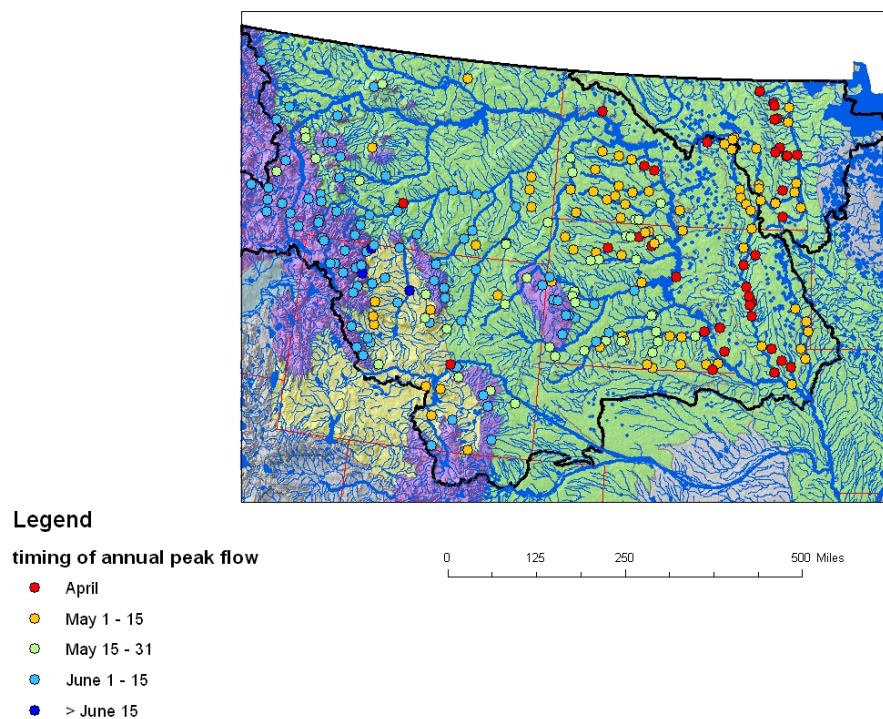
A. Timing (mean Julian day) of annual peak flow.

Legend

variability in timing of annual peak flow

- 🔵 < 2 weeks
- 🔵 2 - 4 weeks
- 🟢 4 - 6 weeks
- 🟠 6 - 8 weeks
- 🔴 > 8 weeks
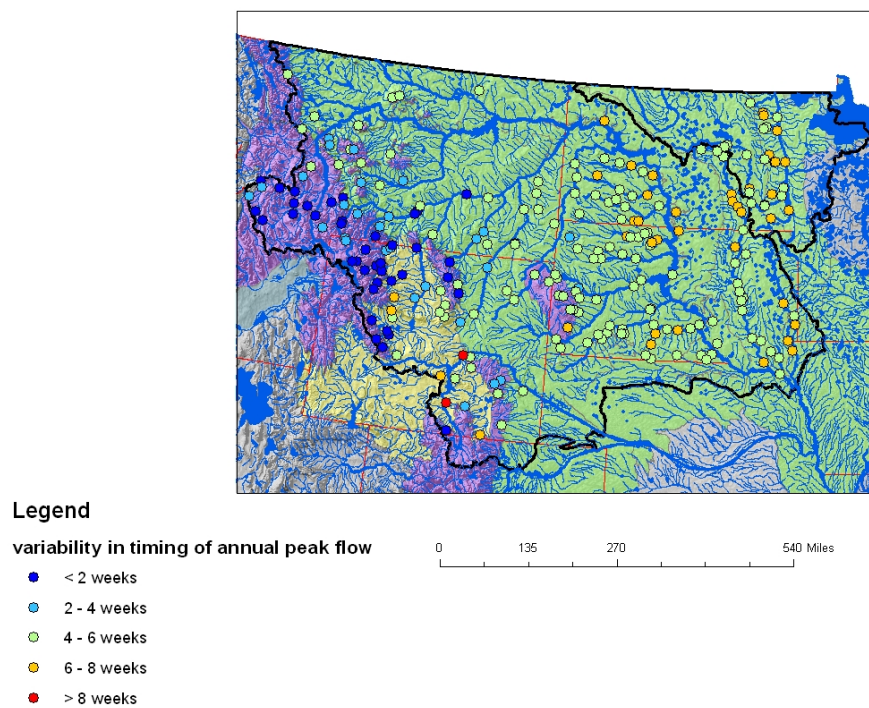
B. Variability (coefficient of variation for mean Julian day) in timing of annual peak flow.

Legend

variability in peak-flow magnitude

- < 2
- 2 - 4
- 4 - 6
- 6 - 8
- > 8
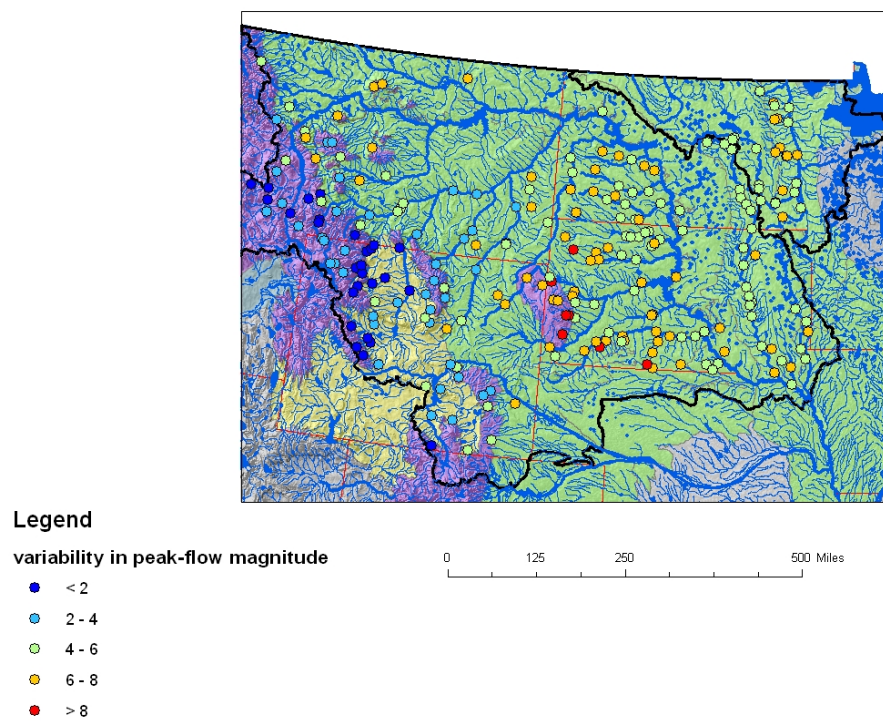
C. Variability (index of dispersion, normalized Q2-Q100) of annual peak flow.

Legend

probability of intermittent flow

- < 0.10
- 0.1 - 0.3
- 0.3 - 0.6
- 0.6 - 0.9
- > 0.9
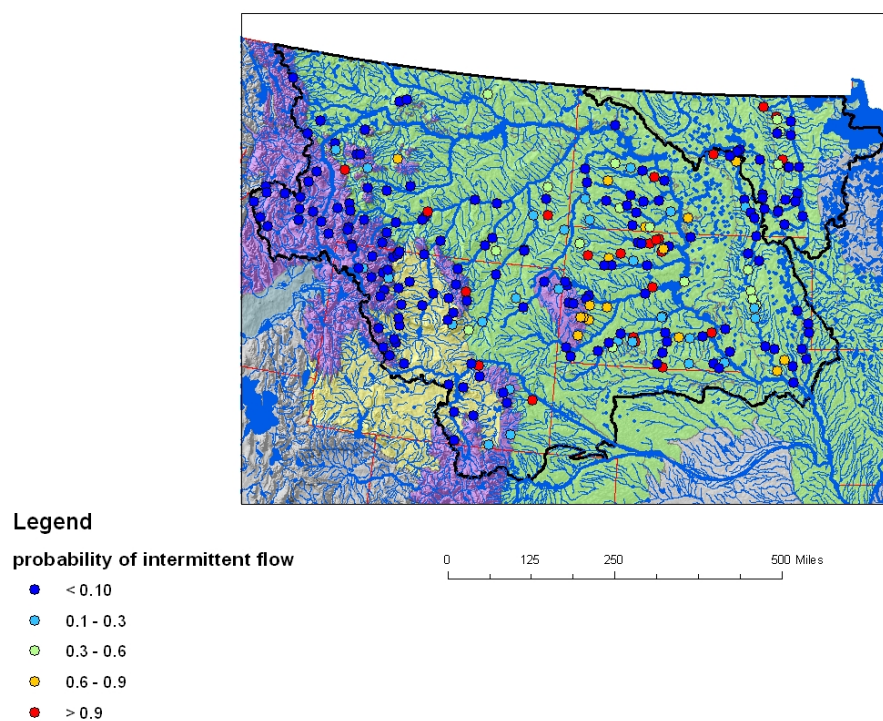
D. Probability of intermittent flow (7-day low flow < 0.5 cubic feet per second).

Ecological trait conservatism and co-occurrence in stream fish assemblages
Introduction

      A significant challenge in community ecology is understanding the relative influence of two primary ecological forces in determining local assemblage composition. The first of these is environmental filtering, whereby species occur together in locations because of a shared fitness advantage derived from the favorable characteristics of physical habitat (Poff, 1997). The second is competition, where species may exclude one another because they share critical habitat resources when those resources are limited in supply (MacArthur and Levins, 1967; Leibold, 1998). An additional consideration is the role of scale, given the understanding that multiple interacting factors govern species distribution patterns across a range of spatial and temporal scale (Ricklefs and Schluter, 1993). These factors have been proposed to act within a hierarchical organization framework to constrain species occurrence based on specific functional attributes (Poff, 1997). Analysis of functional attributes, or ecological traits, of component species provides a more general and predictive science for understanding assemblage structure than simple species identity (McGill and others, 2006). Nonetheless, simple examination of distribution patterns for species and their traits is not sufficient to resolve the question of the dominant mechanisms creating those patterns because of the influence of evolutionary history (Wiens and Graham, 2005).

      The question of rules for assemblage structure relies on the fundamental concept of species niche, which is assumed to describe the biological and physical conditions that support the existence and persistence of a species in a particular locale or habitat (Hutchinson, 1957). The niche is generally considered to be evolutionarily conserved for closely-related species, which implies that the relevant ecological traits will be similarly conserved (Poff and others, 2006). Evolutionarily conserved traits may result in inconsistent patterns of species distribution, depending upon the relative importance of environmental filtering versus competition (Webb and others, 2002). Phylogenetic clustering is expected to occur when highly conserved traits are influenced significantly by environmental filtering, while phylogenetic overdispersion is expected when competitive exclusion is the dominant process. Conversely, where

certain niche components are not conserved within a lineage but evolutionarily more labile, the associated traits will not be strongly linked to phylogenetic relatedness; environmental filtering may cause these traits to converge among less-closely related species. As a consequence, the relative conservatism of ecological traits provides important context for interpreting species patterns, and especially in recognizing the important underlying mechanisms.

This paper describes the evaluation of a small but relatively comprehensive suite of ecological traits (including life history and presumed habitat based on morphology) that describe important components of species niche, and their distribution within stream fish assemblages at two levels of spatial scale. It incorporates the role of phylogenetic history to articulate the influence of these two ecological forces on species co-occurrence patterns across a broad range of physical habitat according to the following conceptual model (Webb and others, 2002)—

	Trait similarity within communities	
Trait evolution	*Clustering of traits— driven by environmental filtering*	*Overdispersion of traits— driven by competitive exclusion*
Conserved	Phylogenetic clustering	Phylogenetic overdispersion
Convergent	Phylogenetic overdispersion	Random dispersion

Theoretically, environmental filtering (i.e. abiotic) and competitive exclusion (i.e. biotic) forces are associated with contrasting expectations about the similarity of traits within communities. As described above, when abiotic forces are more important in structuring an assemblage relevant to a suite of traits, the environment acts like a filter to cluster species with similar traits together. If these traits are strongly conserved within a phylogenetic lineage, phylogenetic clustering is expected to occur—that is, species that are more closely related will be likely to occur together. By comparison, when the important ecological traits are phylogenetically convergent rather than conserved, environmental filtering is expected to result in phylogenetic overdispersion, or co-occurrence of species that are less closely related. In contrast, species are expected to be phylogenetically overdispersed relevant to conserved traits where competitive interactions are most important and randomly distributed for

convergent traits when the phylogenetic signal is disrupted by competitive exclusion (Leibold, 1998; Webb and others, 2002; Davies, 2006).

The study area for this project is the upper Missouri River Basin, encompassing tributaries to the Missouri River in Montana, Wyoming, North and South Dakota (Figure 3.1). These streams are associated with a wide range in elevation and climate patterns, ranging from high elevation sites in the Rocky Mountains to lowland streams in the Great Plains. Accordingly, the underlying regional streamflow patterns differ considerably along this gradient in topography and climate, primarily related to the characteristics of peak flow (Kelly and Jett, 2006). Streams are dominated by snowmelt at high elevation, which generally gives rise to a single prolonged high flow event that occurs predictably in the late spring and early summer, while streams in the plains are dominated by unpredictable thunderstorms that arise suddenly and without warning, generating intense and flashy peak flows (Poff and Ward, 1989).

Several prior studies have proposed a suite of ecological traits that are assumed to respond to environmental filtering by this gradient of flow dynamics (Poff and Ward, 1989; Poff and Allan, 1995; Townsend and Hildrew, 1994; Zeug and Winemiller, 2007). In general, since fish spawning in streams is closely linked to flow conditions, many of these traits are related to the ability of the species to reproduce successfully under a range of flow conditions. Life-history traits, or reproductive strategies, essentially determine the return time for species to recover by reproduction from flow disturbances. Various predictions have been made about reproductive characteristics of species associated with characteristic frequencies of disturbance: i.e. species with short life spans and rapid population growth are expected to thrive in temporally variable conditions, while slow-growing and long-lived species are proposed to persist in more stable and predictable environments (Poff and Ward, 1989; Townsend and Hildrew, 1994). These predictions provide the context for the life-history component of this analysis. Species morphology generates an alternative ecological definition, one based on the utilization of resources. The basic assumption is that ecological relationships between species can be appropriately inferred from their morphological characteristics, utilizing the relationship between form and

function (Winemiller, 1991). A body shape with a high degree of ventral flattening, for example, is likely to be associated with a benthic fish living in fast water (Hora, 1930). Conversely, a relatively deep body shape indicates life in a slow-water habitat (Gatz, 1979).

This paper presents an evaluation of the previously defined conceptual model linking phylogenetic history with co-occurrence of species and their ecological traits. Co-occurrence will be examined at two levels of spatial scale: the local scale is defined by reach-level co-occurrence; the regional scale is defined by co-occurrence within large-scale hydrologic regions. These regions will be defined as aggregates of contiguous watersheds, tributary to the mainstem Missouri River (Figure 3.1). As such, they represent distinct regions subject to a range of climate and topography that are nonetheless highly connected, and therefore linked by a common regional species pool. Species co-occurrence patterns will be examined in the context of phylogenetic relatedness in order to identify the underlying mechanism of coexistence at these two levels of spatial scale, based upon the logical framework described above (Webb and others, 2002).

Methods

Study area   This study is based on data from the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Program (EMAP), which is focused on describing ecological conditions in streams across 12 western states (Stoddard and others, 2005). A total of 247 sites in the upper Missouri River Basin were sampled during the summer low-flow season in 2001-2004 for a wide range of ecological variables, including riparian vegetation, channel conditions, invertebrates, and fish (Peck and others, 2006). EMAP sample sites are stream reaches that are comprised of a length of stream channel 100 times as long as the wetted channel width at the time of sampling (Stoddard and others, 2005). Fish identification and abundances were collected by electrofishing or seining the entire channel within the channel reach. Because fish abundance is expected to vary significantly over the sampling period, analysis was limited to presence/absence only, which is expected to remain fairly constant over this time frame (Matthews and others, 1988; Rahel 1990; Decker and Erman, 1992). Adventitious streams, i.e. small tributary stream reaches

less than 16 kilometers from confluence with large streams (Strahler stream order of 6 or greater), were omitted from the analysis. Further sub-setting of sites according to species composition, described below, resulted in a final set of 100 sites (Figure 3.1).

Hydrologic regions for the regional analysis were defined by the U.S. Geological Survey system of hydrologic units (Seaber and others, 1987). Subregions (4-digit hydrologic units) of the Missouri region were aggregated to form three large-scale hydrologic regions as follows: Yellowstone (1007, 1008, 1009, 1010), White-Little Missouri (1011, 1012, 1013, 1014), and James-Big Sioux (1016, 1017) (Figure 3.1).

The study area varies greatly in terms of several major environmental gradients that are important to fishes. Topography ranges from the Rocky Mountains in the west, characterized by perennial snowmelt streams, to the broad and xeric intermontane high plateau of the Wyoming Basin, and further east to the lowlands of the Great Plains where stream slopes can be much less than 1 percent. Channel substrate changes considerably over this topography gradient, with gravels dominating in mountain streams and very fine sand prevalent in the lowland streams. Stream size, and corresponding water volume, also varies greatly: sampled reaches ranged from small first-order headwater streams to large eighth-order rivers such as the Yellowstone.

Phylogenetic analysis The phylogeny of fishes is complex and, despite being studied in detail for many species, is incompletely resolved across the range of species observed within the study area. The analysis was focused on native and common species only, defined as comprising at least 20 percent of the total number of individuals at any single site. Estimation of phylogenetic relationships was additionally limited to three major families: Catostomidae, Cyprinidae, and Ictaluridae (Table 3.1). These families were selected because they are relatively closely related, the first two within the same order (Cypriniformes), and both orders (Cypriniformes and Siluriformes) located within the surperorder Ostariophysi. Accordingly, a minimum of assumptions was required to generate a community phylogeny from literature sources.

A phylogenetic "supertree" was estimated by joining results from several phylogenies from literature studies, based on morphology (Coburn and Cavender, 1992; Lundberg, 1992; Nelson, 2006; Smith, 1992). Branch lengths for this analysis were estimated based on a modification of the method described by Grafen (1989), where phylogenetic distance is simply the sum of nodes separating two taxa. In this case, all pair-wise distances between species were normalized by the maximum number of nodes between species within the family Cyprinidae, which contained the largest number of species. As a result, all nodes between species within a single family were assumed to be the same length; nodes between families and between orders were set equal to one. In this way, inter-specific distances between species in different families always exceed differences within a family, and differences between orders always exceed differences within the same order.

Phylogenetic distance and co-occurrence within assemblages To evaluate the presence of phylogenetic clustering or overdispersion in fish assemblages, we determined whether there was a significant correlation between the phylogenetic distance between species pairs and their degree of co-occurrence; separate analysis was conducted for local and regional co-occurrence. Presence/absence data were utilized for the co-occurrence analysis, rather than density based on number of individuals, because the multi-year sampling time frame required an emphasis on large-scale distribution patterns rather than smaller-scale variability in population size. Phylogenetic distance was defined as the sum of estimated lengths of all intervening branches between two species on the phylogenetic tree. Pair-wise co-occurrence was calculated using an index based on proportional similarity (Schoener, 1970) as follows: $CI_{ih} = 1 - 0.5 \times \Sigma |p_{ij} - p_{hj}|$ where CI_{ih} is the co-occurrence of species i and h and p_{ij} is the proportion of occurrences of the ith species in the jth sample. Values range from 0 (species never occur together) to 1 (species always occur together). Matrices containing phylogenetic distances and CI for all species pairs were determined by the program Ecophyl, obtained from the University of Minnesota (Cavender-Bares and Lehman, personal communication, 2007).

A Mantel test was conducted to evaluate the correlation between the two matrices; the significance of the correlation was determined from the distribution of

correlation coefficients generated by a null or randomized model where rows and columns of the phylogenetic distance matrix were shuffled 999 times to randomize the phylogenetic distance scores. Mantel's Z statistic from the non-randomized data was compared to the distribution of Z statistics from the shuffled data, and a p-value was determined from the number of occurrences where the test statistic from the randomized data was equal to or more extreme than the observed value. The association between the two matrices can be either negative or positive. The Mantel test was conducted by PC-ORD (McCune and Mefford, 1999). Based on a two-tailed test, a negative correlation relative to the null model was assumed to represent phylogenetic clustering (i.e. co-occurring species are more closely related); a positive correlation represented phylogenetic overdispersion.

Life-history and ecomorphological traits Ecological traits were selected to represent two major niche components: life history and habitat utilization (Table 3.2). Most life-history traits and trophic level data were acquired from FishBase, a relational database on the web that was developed at the World Fish Center in collaboration with the United Nations and other partners (Froese and Pauly, 2007). Additional data were provided from the Depository of Unpublished Data, CISTI, National Research Council of Canada (Winemiller and Rose, 1992). Data were selected to represent different life-history strategies as comprehensively as possible, given the incompleteness of available data for some parameters. Morphological data were obtained from measurements of museum specimens at the Division of Ichthyology, Natural History Museum and Biodiversity Research Center of the University of Kansas. Because species may exhibit significant phenotypic plasticity in morphological traits across their geographic range, specimens were selected from samples collected as close as possible to the center of their range within the study area. Measurements were made using vernier calipers to the nearest 0.1 mm (measures < 130 mm), and to the nearest 1 mm with a ruler (measures > 130 mm). Three specimens of adult size were measured for each species, and values were expressed as the mean. Measurements were done according to methods described in Winemiller (1991).

The dominant patterns of variability among life-history traits and morphological traits were examined by principal components analysis. Trait values were normalized prior to the analysis by the maximum value observed for each trait. Euclidian distances were evaluated, based on a cross-product matrix containing correlation coefficients. The significance of the eigenvalue for each component was evaluated relative to a broken-stick model. Only those components with eigenvalues greater than the broken-stick eigenvalue were considered to contain more information than expected by chance.

Convergence and conservatism of traits Convergence or conservatism of ecological traits was tested by examining correlations between pair-wise trait differences and phylogenetic distance between species (Cavender-Bares and others, 2004). Matrices of pair-wise trait differences were determined in Excel, and Mantel tests were conducted as described above. Trait conservatism was suggested by a positive correlation relative to the null model, i.e. greater differences in traits were associated with larger phylogenetic distances, while trait convergence was suggested by a negative correlation.

Trait clustering and overdispersion Matrices containing pair-wise trait differences and species co-occurrence were correlated by using the Mantel test to determine whether either phenotypic clustering or overdispersion could be determined for both local or reach-level and regional co-occurrence. For this comparison, phenotypic clustering was identified by a significant negative correlation, i.e. species that co-occur more frequently were more similar. Conversely, phenotypic overdispersion was suggested by a significant positive correlation, where co-occurring species were less similar.

Results

The great majority of species pairs never occurred together locally (Figure 3.2A), and generally the level of local co-occurrence was low. Of 466 total species pairs, 324 or 70 percent had CI values of zero, and all but 1 had CI values < 0.5. Local co-occurrence tended toward a more positive correlation with phylogenetic distance than expected (the correlation was only marginally significant, with standardized Mantel statistic r=0.09, p=0.10). The positive relationship implies that

more distantly-related species may co-occur more frequently than expected by chance, and that more closely-related species tend to not occur together, suggesting phylogenetic overdispersion.

In contrast, regional co-occurrence showed a greater range in variation than was observed for local-occurrence (Figure 3.2B). Only 50 species pairs (about 11 percent) had CI values of zero, while 295 pairs (67 percent) had CI values of at least 0.5. No significant pattern of phylogenetic relatedness was observed for regional co-occurrence (r=0.02, p=0.53).

Results from the ecological trait PCA show strong separation along the first PCA ordination axis, defined primarily by life-history traits (Figure 3.3). Results are shown for the first two principal components, although only the first component was significant based on the broken-stick model. The first axis describes the gradient described by growth rate, age at maturity, life span, generation time, and partially by length of spawning season. Body shape, as described by relative body depth and the degree of ventral flattening, and ovum size were the major components of the second axis. Species were generally separated according to family membership within the trait space defined by the ordination, with Cyprinidae associated with relatively fast growth rates, short life spans, early age at maturity, short generation time and long spawning season. Catostomidae was associated with the reverse, while Ictaluridae was somewhat intermediate relative to this axis. The second axis essentially described the separation of Ictaluridae from the others relative to body shape (more ventrally flattened) and larger ovum size.

Significant patterns of phylogenetic relatedness were observed for most ecological traits, including both life history (life span, generation time, age at maturity, and ovum size) and habitat-related traits (trophic level, mouth position, peduncle length, and ventral flattening) (Table 3.4). These traits were all associated with positive correlations with phylogenetic distance, indicating that more closely-related species are more similar, i.e. that these traits describe niche dimensions that are evolutionarily conserved. No significant negative correlations were observed, implying that no phylogenetic convergence of traits was detected for this group of species.

Contrasting patterns were observed for local and regional scales of phenotypic co-occurrence (Table 3.4). A significant and positive correlation with CI was found for trophic level at the local scale, indicating phenotypic overdispersion; mouth position showed a similar tendency but was only marginally significant. Body depth was also marginally but negatively correlated with CI at the local level, indicating a tendency toward phenotypic clustering. Among life history traits, only ovum size showed a significant correlation with local co-occurrence. These results imply that species tend to separate from one another at the local scale if they are similar in feeding strategy, while they tend to cluster together according to similar body shape (a surrogate for habitat preference to water velocity). While life-history traits were more strongly conserved than expected by chance, they provided essentially no information on how species were distributed to each other at the local scale. The only ecological traits that showed clear evidence for non-random patterns between co-occurring species at the local scale were those related to habitat, specifically body depth, trophic level, and mouth position (Figure 3.4A). In contrast, significant and positive correlations were observed for most life-history traits with regional co-occurrence, including growth rate, life span, age at maturity, and generation time (Table 3.4). These results imply that large-scale environmental filtering is occurring so that species tend to cluster together regionally if they share similar life-history strategies (Figure 3.4B).

Discussion

Several patterns are immediately apparent from these results: first, most of the selected ecological traits are strongly evolutionarily conserved, and none are convergent across the range of phylogeny evaluated here (Table 3.4, Figure 3.4). The relative conservatism of life-history traits is consistent with the strong PCA gradient of families that was observed for these traits (Figure 3.3). These results imply a gradient in life-history strategy that is phylogenetically constrained across the set of species, where certain combinations or suites of traits are strongly associated with certain closely related species (Poff and others, 2006).

Second, species co-occurrence patterns varied significantly between the local and regional scale (Figure 3.2). At the reach level, only a small number of species

pairs occurred together, while a more variable range of coexistence was observed for species at the regional scale. Most species pairs co-occurred within regions with some moderate frequency, reflecting the broader geographic distribution of species coexistence at the larger scale.

Similar contrasting results were observed for the analysis of phenotypic co-occurrence across the range of scale (Table 3.4, Figure 3.4). Locally, we found significant positive correlations between phenotypic difference and co-occurrence relative to two traits: trophic level and ovum size, indicating phenotypic overdispersion; a tendency toward overdispersion was also observed for mouth position and body depth (Figure 3.4A). Phenotypic overdispersion, where similar species do not occur together, relative to trophic level was consistent with the possibility that feeding competition is an important factor structuring fish coexistence at the reach scale. Overdispersion relative to ovum size may simply be a spurious association with trophic level (Figure 3.3), or may reflect more complex associations among species based on competition for spawning sites.

At the regional scale, on the other hand, we found correlations between phenotypic differences and co-occurrence to be more negative than expected by chance, indicating phenotypic clustering for many life-history traits including growth rate, life span, generation time, and age at maturity; similar negative correlations were observed for eye position, and marginally significant tendencies toward clustering for body depth and peduncle length (Table 3.4, Figure 3.4). Phenotypic clustering for life-history traits at the regional scale implies that large-scale physical habitat features serve to constrain the distribution of life-history strategies. The range of climate and topography, and coincident streamflow regime, are likely to be important components of these regional factors.

Finally, the signature of phylogenetic overdispersion between co-occurring species was marginally detectable at the local scale (p=0.10), but we found no phylogenetic pattern different from that expected by chance at the regional scale (p=0.53). According to the conceptual model evaluated here, phylogenetic overdispersion is expected when phenotypic overdispersion occurs for highly conserved traits, and reinforces the interpretation that ecologically similar species

locally exclude each other via competition. The lack of phylogenetic signal at the larger scale is not possible to resolve with the present data, but is consistent with results observed for other species (Lovette and Hochachka, 2006). If the present conceptual model is correct, phenotypic clustering of conserved traits at the regional scale should be associated with phylogenetic clustering. However, it has been proposed that long-term variability in species ranges, such as has occurred in the Missouri River Basin due to large-scale climate cycles, tends to obscure the underlying speciation patterns so that a clear large-scale phylogenetic signal cannot be detected (Losos and Glor, 2003). In any case, these differences between local and regional species co-occurrence patterns clearly suggest that spatial scale is a critical consideration in determining the important ecological forces that determine assemblage structure.

Unambiguous differences exist between species co-occurrence patterns at the local and regional scale for stream fish assemblages, both regarding the relevant ecological traits and the extent of phenotypic clustering versus overdispersion (Figure 3.4). Locally, fish coexistence may be mediated significantly by present or past competition, leading to spatial segregation of species when they share similar feeding strategies. Because trophic level is strongly conserved within phylogenetic lineages, the result is phylogenetic overdispersion at the local scale, or co-occurrence within stream reaches of species that are less closely related. These results imply that biotic interactions are more important than environmental filtering at the local scale. At the regional scale, a contrasting pattern occurs, based apparently on the response of life-history strategies to large-scale physical habitat filters so that similar species tend to cluster together within regions. While these traits are highly constrained and correlated with one another, the phylogenetic signal for regional coexistence is not detectable for this group of species.

These results provide an application of the phylogenetic and trait-based approach to developing insight into mechanisms that underlie fish assemblage structure in streams. They especially underline the importance of a multi-scale perspective, whereby large- and small-scale factors interact to constrain species distribution patterns. The mode of feeding provides an important local niche

dimension whereby similar species are segregated from one another. Life-history strategies define another critical niche dimension that operates to cluster similar species at the regional scale, presumably in accordance with large-scale climate and topography. Taken together, these results indicate that species distribution patterns, and resulting assemblage structure, results from the simultaneous influence of processes and interactions at different levels of scale. Furthermore, these factors not only differ but apparently oppose one another across scale. This approach, therefore, provides valuable context for distinguishing the relative influence of local and regional forces on stream fish assemblages.

References

Bunn, S.E., and A.H. Arthington, 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30(4): 492-507.

Cavender-Bares, J,. D.D. Ackerly, D.A.Baum, and F.A.Bazzaz, 2004. Phylogenetic overdispersion in Floridian oak communities. The American Naturalist 163(6): 823-843.

Cavender-Bares, J., A. Keen, and B. Miles, 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. Ecology 87(7) Supplement: S109-S122.

Coburn, M.M. and T.M. Cavender, 1992. Interrelationships of North American cyprinid fishes, pages 329-365 *in* R.L. Mayden, (editor) Systematics, historical ecology, and North American freshwater fishes. Stanford University Press, Stanford CA.

Davies, T.J., 2006. Evolutionary ecology: when relatives cannot live together. Current Biology 16(16): R645-R647.

Decker, L.M. and D.C. Erman, 1992. Short-term seasonal changes in composition and abundance of fish in Sagehen Creek, California. Transactions of the American Fisheries Society 121: 297-306.

Frissell, C.A., W.J. Liss, C.E. Warren, and M.D. Hurley, 1986. A hierarchical framework for stream habitat

Froese, R. and D. Pauly, (eds), 1998. FishBase 1998: concepts, design and data sources. ICLARM, Manila, Philippines. 293 pp.

Froese, R. and D. Pauly, 2007. Editors, FishBase: World Wide Web electronic publication (www.fishbase.org).

Gatz, A.J., 1979. Community organization in fishes as indicated by morphological features. Ecology 60(4): 711-718.

Grafen, A., 1989. The phylogenetic regression. Philosophical Transactions of the Royal Society of London, Series B 326: 119-157.

Hora, S.L., 1930. Ecology, bionomics and evolution of the torrential fauna, with species reference to the organs of attachment. Philosophical Transactions of the Royal Society 28: 171-282.

Hutchinson, G.E., 1957. Concluding remarks. Cold Spring Harbor Symposium in quantitative biology. Volume 22: 415-427.

Kelly, V.J. and S.M, Jett, 2006. Ecologically relevant quantification of streamflow regimes in western streams. EPA/600/ R-06/056.

Leibold, M., 1998. Similarity and local coexistence of species in regional biotas. Evolutionary Ecology 12: 95-100.

Losos, J.B. and R.E. Glor, 2003. Phylogenetic comparative methods and the geography of speciation. Trends in Ecology and Evolution 18(5): 220-227.

Lovette, I.J. and W.M. Hochachka, 2006. Simultaneous effects of phylogenetic niche conservatism and competition on avian community structure. Ecology 87(7) Supplement: S14-S28.

Lundberg, J.G., 1992. The phylogeny of ictalurid catfishes: a synthesis of recent work, pages 392-411 *in* R.L. Mayden, (editor) Systematics, historical ecology, and North American freshwater fishes. Stanford University Press, Stanford CA.

MacArthur, R. and R. Levins, 1967. The limiting similarity, convergence and divergence of coexisting species. The American Naturalist 101: 377-385.

Matthews, W.J., R.C. Cashner, and F.P. Gelwick, 1988. Stability and persistence of fish faunas and assemblages in three Midwestern streams. Copeia 1988: 947-957.

McCune, B. and M.J. Mefford, 1999. PC_ORD. Multivariate analysis of ecological data, version 4. MjM Software Design, Gleneden Beach, Oregon, USA.

McGill, B.J., B.J. Enquist, E. Weiher, and M.Westoby, 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21: 178-185.

Nelson, J.S., 2006. Fishes of the world. John Wiley, Hoboken NJ.

Peck, D.V., Herlihy, A.T., Hill, B.H., Hughes, R.M., Kaufmann, P.R., Klemm, D.J., Lazorchak, J.M., McCormick, F.H., Peterson, S.A., Ringold, P.L., Magee, T., Cappaert, M., 2006. Environmental Monitoring and Assessment Program-Surface Waters Western Pilot Study: Field Operations Manual for Wadeable Streams. EPA/620/R-06/003, U.S. Environmental Protection Agency, Office of Research and Development, Washington, DC.

Poff, N.L., 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of North American Benthological Society 16: 391-409.

Poff, N.L., and J.D. Allan, 1995. Functional organization of stream fish assemblages in relation to hydrological variability. Ecology 76(2): 606-627.

Poff, N.L., and J.V. Ward, 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Canadian Journal of Fisheries and Aquatic Sciences 46: 1805-1817.

Poff, N.L., J.D. Olden, N.K.M. Vieira, D.S. Finn, M.P. Simmons, and B.C. Kondratieff, 2006. Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. Journal of North American Benthological Society 25(4): 730-755.

Rahel, F.J., 1990. The hierarchical nature of community persistence: a problem of scale. The American Naturalist 136: 328-344.

Raley, M.E. and R.M. Wood, 2001. Molecular systematics of members of the *Notropis dorsalis* species group (Actinopterygii: Cyprinidae). Copeia 200(3): 638-645.

Resh, V.H., A.V. Brown, A.P. Covitch, M.E. Gurtz, H.W. Li, G.W. Minshall, S.R. Reice, A.L. Sheldon, H.B. Wallace, and R.C. Wissmar, 1988. The role of disturbance in stream ecology. Journal of North American Benthological Society 7: 433-455.

Ricklefs, R.E. and D. Schluter, 1993. Species fiversity in ecological communities. University of Chicago Press, Chicago, Illinois.

Schoener, T.W., 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51: 408-418.

Seaber, P.R., F.P. Kapinos, and G.L. Knapp, 1987. Hydrologic unit maps. U.S. Geological Survey Water-Supply Paper 2294.

Smith, G.R., 1992. Phylogeny and biogeography of the Catostomidae, freshwater fishes of North America and Asia, pages 778-827 *in* R.L. Mayden, (editor) Systematics, historical ecology, and North American freshwater fishes. Stanford University Press, Stanford CA.

Southwood, T.R.E., 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology 46: 337-365.

Stoddard, J.L., Peck, D.V., Paulsen, S.G., Van Sickle, J., Hawkins, C.P., Herlihy, A.T., Hughes, R.M., Kaufmann, P.R., Larsen, D.P., Lomnicky, G., Olsen, A.R., Peterson, S.A., Ringold P.L., Whittier, T.R., 2005. An Ecological Assessment of Western Streams and Rivers. EPA 620/R-05/005, U.S. Environmental Protection Agency, Washington, DC.

Townsend, C.R., and A.G. Hildrew, 1994. Species traits in relation to a habitat templet for river systems. Freshwater Biology 31: 265-275.

Webb, C.O., D.D. Ackerly, M.A. McPeek, and M.J. Donoghue, 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics 33: 475-505.

Wiens, J.J. and C.H. Graham 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology and Systematics 36: 519-539.

Winemiller, K.O., 1991. Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. Ecological Monographs 61(4): 343-365.

Winston, M.R., 1995. Co-occurrence of morphologically similar species of stream fishes. The American Naturalist 145(4): 527-545.

Table 3. 1. Native and common species in three major families.

Species name	Common name
Family Catostomidae	
Carpiodes carpio	River carpsucker
C. cyprinus	Quillback
Catostomus catostomus	Longnose sucker
C. commersonii	White sucker
C. platyrhynchus	Mountain sucker
Ictiobus cyprinellus	Bigmouth buffalo
Moxostoma macrolepidotum	Shorthead redhorse
Family Cyprinidae	
Couesius plumbeus	Lake chub
Cyprinella lutrensis	Red shiner
C. spiloptera	Spotfin shiner
Hybognathus argyritis	Western silvery minnow
H. hankinsoni	Brassy minnow
H. placitus	Plains minnow
Luxilus cornutus	Common shiner
Macrhybopsis gelida	Sturgeon chub
M. meeki	Sicklefin chub
Margariscus margarita	Pearl dace
Notropis atherinoides	Emerald shiner
N. dorsalis	Bigmouth shiner
N. hudsonuis	Spottail shiner
N. stramineus	Sand shiner
Phoxinus eos	Northern redbelly dace
Pimephales notatus	Bluntnose minnow
P. promelas	Fathead minnow
Platygobio gracilis	Flathead chub
Rhinichthys atratulus	Blacknose dace
R. cataractae	Longnose dace
Semotilus atromaculatus	Creek chub
Family Ictaluridae	
Amerius melas	Black bullhead
Ictalurus punctatus	Channel catfish
Noturus flavus	Stonecat

Table 3. 2. Summary of life-history, ecological and morphological traits.

Life-history traits	
Bertalanffy k [1]	Rate (1/year) at which the asymptotic length is approached, based on $L_t = L_\infty (1 - e^{-k(t-t_0)})$ where L_t is the length at age t, L_∞ is the asymptotic length of the individual, and k is the von Bertalanffy growth rate
Life span [1]	Approximate maximum age (years), calculated as the age at 95% of L_∞
Generation time [1]	Mean age (years) of parents at the time their young are born (t_g), (assumed to be the size class with the maximum egg production), calculated using the parameters of the von Bertalanffy growth function $t_g = t_{opt} = t_0 - \ln(1 - L_{opt} / L_\infty) / k$
Age at maturity [1]	Mean age (years) at which fish of a given population mature for the first time, calculated from the length at first maturity using the inverse of the von Bertalanffy growth function $t_m = t_0 - \ln(1 - L_m / L_\infty) / k$
Ovum size [2]	Mean diameter of mature (fully yolked) ovarian oocytes (to nearest 0.01 mm)
Spawning season [2]	Number of days that spawning or early larvae were reported
Ecological and morphological traits	
Trophic level [1]	Rank of the species in a food web, estimated as 1 + mean trophic level of food items (weighted by the contribution of the various food items)
Mouth position [3]	Coded: 1=superior; 2=terminal; 3=inferior; 4=bottom
Body depth [3]	Maximum body depth / standard length
Peduncle length [3]	Caudal peduncle length / standard length
Ventral flattening [3]	Proportion of body depth below the midline at the point of maximum depth
Eye position [3]	Proportion of head depth at the middle of the eye, occurring below the middle of the eye
[1] FishBase, Froese and Pauly, 1998; [2] CISTI, Winemiller and Rose, 1992; [3] Measurements from KU Museum; see text for explanation of data sources	

Table 3. 3. Principal component statistics for life-history and ecological traits.

Axis	Eigenvalue	Percent of variance	Broken-stick eigenvalue
1	5.108	42.5	3.103
2	1.974	16.4	2.103

Table 3. 4. Test of trait evolution and co-occurrence at two levels of spatial scale.
[local defined by sample reach; region defined by large-scale hydrologic region; see text for further details]

Trait	Phylogenetic distance		Local co-occurrence		Regional co-occurrence	
	R	p	R	p	R	p
Life-history traits						
Bertalanffy *k*	0.16	0.03 *	-.02	0.38	-0.14	0.04 *
Life span	0.29	0.03 *	-0.02	0.45	-0.27	0.02 *
Generation time	0.28	0.04 *	-0.009	0.48	-0.26	0.03 *
Age at maturity	0.28	0.04 *	-0.01	0.42	-0.26	0.02 *
Ovum size	0.73	0.001 *	0.13	0.03 *	0.006	0.57
Length of spawning season	0.05	0.41	0.02	0.41	-0.03	0.31
Ecological and morphological traits						
Trophic level	0.22	0.03 *	0.14	0.009 *	0.02	0.50
Mouth position	0.07	0.20	0.07	0.12	0.06	0.26
Body depth	0.11	0.21	-0.08	0.13	-0.15	0.08 **
Peduncle length	0.21	0.03 *	-0.05	0.19	-0.10	0.11
Ventral flattening	0.30	0.05 *	0.06	0.22	0.06	0.23
Eye position	0.16	0.04 *	-0.05	0.22	-0.14	0.02 *
* indicates statistical significance at p<0.05; ** indicates marginal significance at p<0.10						

Figure 3. 1. Map of study area, with sample reaches, major ecoregions, and large-scale hydrologic regions.
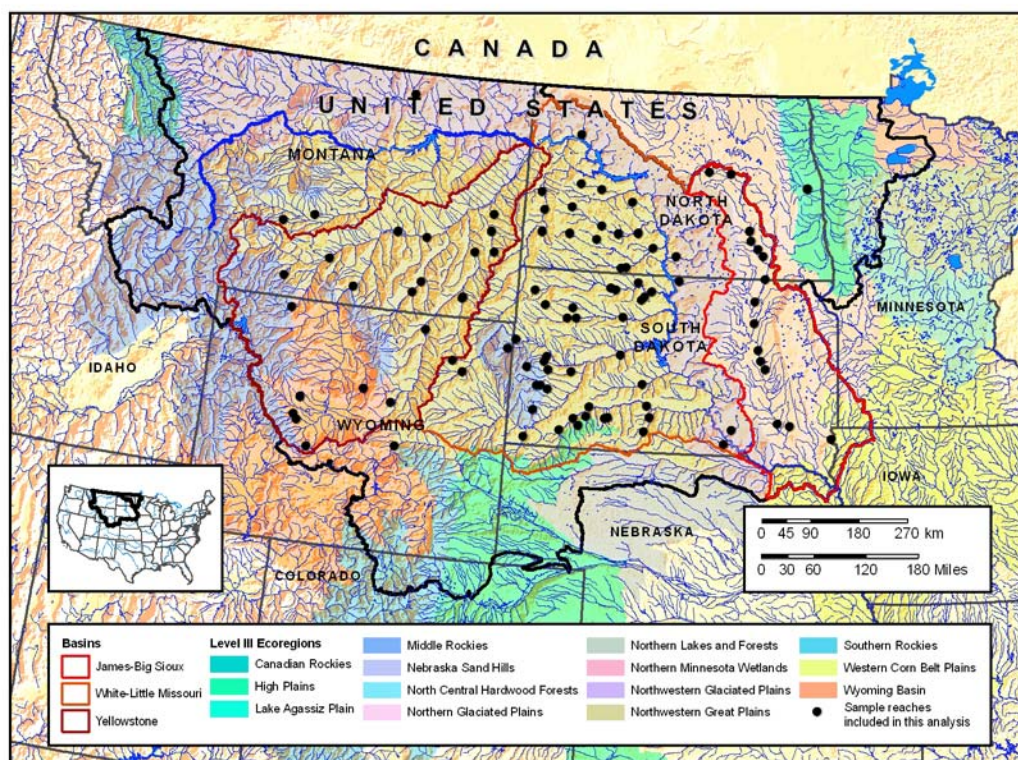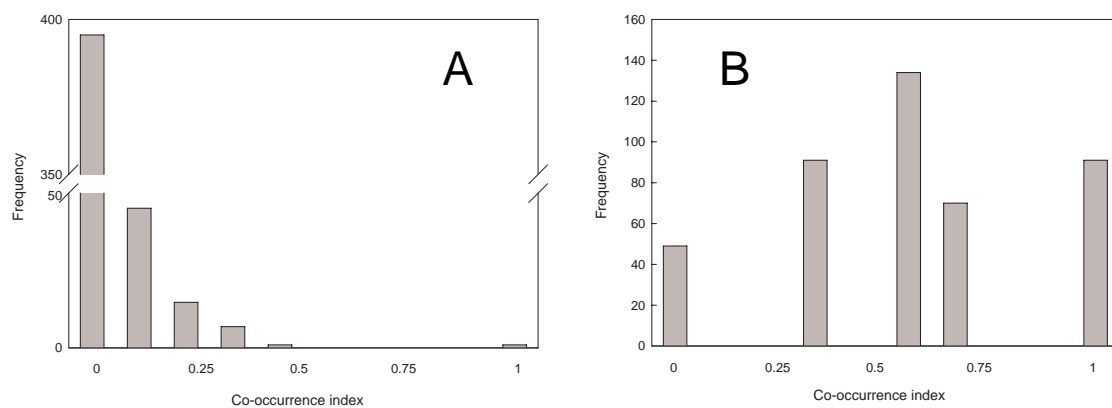
Figure 3. 2. Frequency distribution of the co-occurrence indices for all possible species pairs.
A. Local co-occurrence; B. Regional co-occurrence.

Figure 3. 3. Principal component ordination for fishes, classified by family, on the first two principal component axes based on selected life-history and morphological traits.
Lines indicate the direction and relative strength of correlations of variables with ordination axes.
[N.S. not significant because eigenvalue < broken-stick eigenvalue]
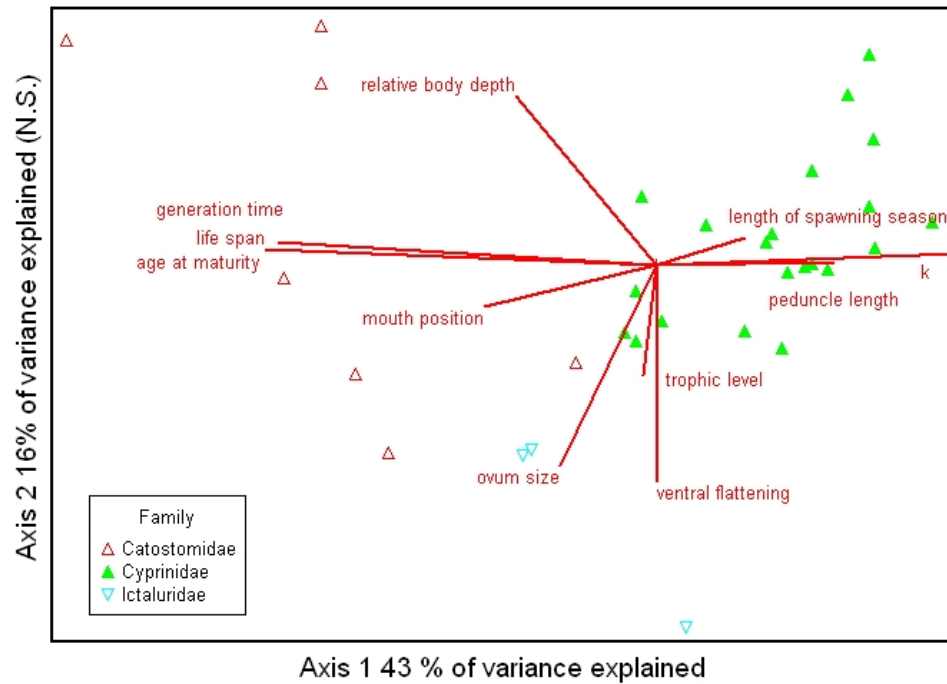
Figure 3. 4. Conservatism of trait evolution in relation to similarity of traits within assemblages.
The axes represent the number of randomized runs with Z less than the observed value for the correlation of species pairwise trait differences with degree of co-occurrence (X-axis) or phylogenetic distance (Y-axis). Dashed lines represent the lines of marginal statistical significance (p=0.10).
A. within local assemblages; B. within large-scale hydrologic regions.
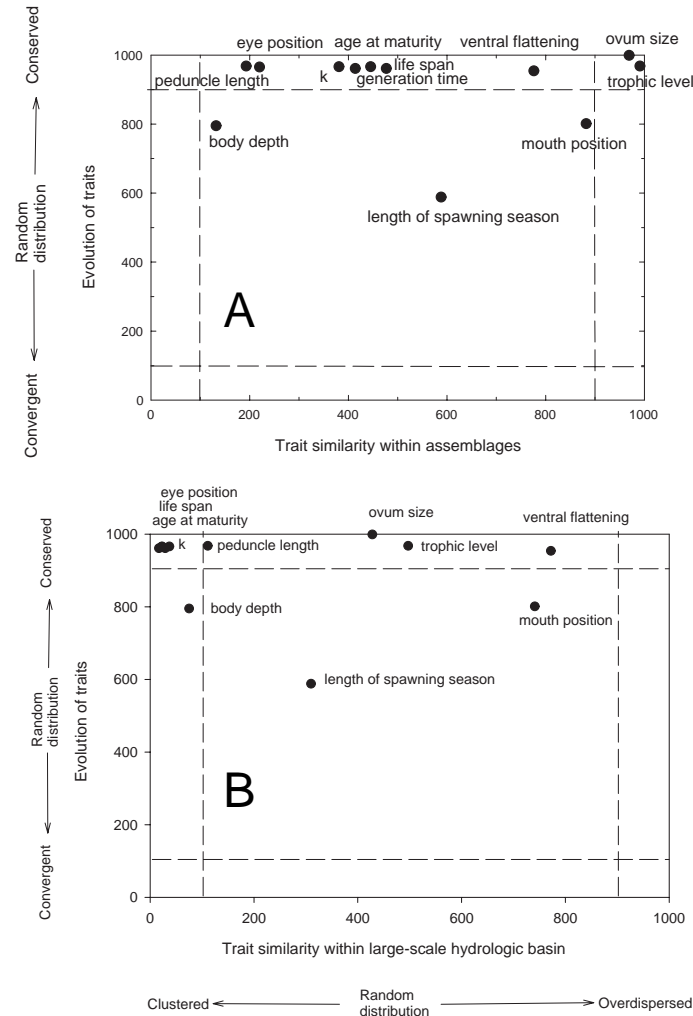
Streamflow regime shapes distribution of life-history strategies across multiple levels of scale in stream fishes

Introduction

Theories about community assembly have historically been based on local considerations and dominated by biological interactions between species pairs (MacArthur, 1968; Tilman, 1976). More recently, the general understanding has expanded to include the interplay of abiotic and biotic factors in determining community structure (Peckarsky, 1983; Diez and Pulliam, 2007), and the occurrence of these factors across multiple levels of scale, with their relative importance dependent upon the scale and focus of the investigation (Wiens, 1989; Levin, 1992). While inter-specific competition is still considered an important influence on species co-occurrence patterns in stream fishes (Winston, 1995), large-scale landscape processes have also been identified as important factors determining local stream fish assemblages (Schlosser, 1991). Still, the interplay of biotic and abiotic processes that result in species distribution patterns is not well understood (Poff, 1997). Specifically, how these ecological processes interact across multiple levels of spatial and temporal scale in stream systems has not been established (Fausch and others, 2002).

Streamflow regime provides a useful perspective for examining the effect of scale on local assemblage structure because distinct patterns of streamflow variability occur across a range of spatial and temporal scale (Biggs and others, 2004). Regional analysis of streamflow in the United States reveals large-scale patterns that are based primarily on variability in flood frequency and predictability (Poff and Ward, 1989). Within large-scale regions, characteristic patterns of flow variability can also be observed across the scale of the stream network, depending on location within the network (Reice and others, 1990; Dodds and others, 2004). At smaller levels of spatial scale, variability in flow characteristics is determined largely by the distribution of physical features within the stream channel (Statzner and others, 1988), The range of spatial scale is also associated with a corresponding temporal scale of variability ranging from decades to years, months to days, and hours to minutes (Biggs and others, 2004).

The characteristic streamflow regime for a given stream reach is widely recognized as a critical ecological and evolutionary template for resident species, especially regarding the development of coincident ecological traits (Resh and others, 1988). Furthermore, species ecological traits have been proposed as an appropriate focus for analysis of community organization, one which can facilitate general and predictable understanding especially when the analysis examines the distribution of traits in response to environmental gradients (McGill and others, 2006). This perspective of habitat as template is grounded in the theory of natural selection, and regards physical habitat as a selective force in structuring species traits by its effect on the relative fitness of individuals (Southwood, 1988). Whether a species can complete their reproductive cycle is obviously important to their success or failure in persisting in a particular environment. Accordingly, analysis of the distribution of reproductive traits in response to streamflow regime provides a useful perspective for understanding the impact of flow regime on the structure of stream fish assemblages.

Reproductive traits are frequently combined into suites of traits described as life-history strategies. These strategies are considered to result from the coordinated evolution of multiple traits together in response to environmental variation (Stearns, 1992). In fishes, suites of reproductive traits have been described by a trilateral continuum of life-history strategies that result from tradeoffs among three primary demographic parameters (onset/duration of reproduction, fecundity, and survival) (Winemiller and Rose, 1992) (Figure 4.1). Each demographic parameter is maximized by a specific strategy or set of traits, which define so-called opportunistic, periodic, and equilibrium strategies. According to this conceptual model, the endpoints or extreme expressions of each fish life-history strategy are associated with distinctive ecological characteristics as follows (Winemiller and Rose, 1992): (1) The opportunistic strategy minimizes generation time by fast growth and early maturity, and is associated primarily with small fishes with relatively small eggs that reproduce over extended spawning seasons. These species are associated with high mortality in the adult stage, either due to frequent disturbances or strong predation pressure. (2) The periodic strategy maximizes fecundity, and is associated with large-bodied fishes that grow slowly, mature later, and lay large numbers of small eggs. These species

frequently depend upon regular large-scale temporal cycles that cue migration to favorable habitats for synchronized spawning. (3) The equilibrium strategy maximizes juvenile survival by a set of characteristics that include moderately small body size associated with relatively slow growth, small numbers of large eggs, and a high level of parental care. It is presumed to be advantageous for species living in resource-limited environments and may be associated with stressful habitat conditions.

The original life-history model also describes characteristic patterns of biotic interactions, specifically inter-specific competition, that are associated with each strategy as follows (Winemiller, 2005): The opportunistic strategy is considered to be a colonizing strategy that is most adaptive under density-independent demographic conditions, subject to high mortality from either disturbance or predation, when inter-specific competition is not important. The periodic and especially the equilibrium strategies are expected to be more adaptive for species subject to increasingly higher levels of competitive pressure.

This study examines the implications of this life-history model for the structure of fish assemblages along a gradient of streamflow regime in the upper Missouri River Basin (Figure 4.2). The distribution of fish species within the study area is described by data from streams sampled by the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Program (EMAP). In this context, fish "assemblages" are defined generically as the group of populations observed within the sample reach.

This analysis examines the trilateral conceptual model for fish life-history strategies (Winemiller and Rose, 1992) within the context of classic habitat template theory (Southwood, 1988). Habitat template theory predicts a characteristic distribution of species in response to three critical axes or dimensions: disturbance, adversity, and biotic interactions (here focusing exclusively on competition) (Figure 4.3). In accordance with this theory, high levels of disturbance are assumed to be associated with ruderal or colonizing species and communities characterized by low niche overlap, indicating low levels of inter-specific competitive interactions (Figure 4.3A). Low levels of disturbance are theoretically characterized by increasing biotic interactions and narrower niche breadth in communities, possibly reflecting higher

levels of competitive interactions. The second axis describes a gradient of adversity or environmental stress, which is negatively related with the biotic axis so that highly adverse conditions are predicted to be associated with reduced competition. The predicted locations of the three fish life-history strategies within the habitat template are described as follows (Figure 4.3B) (Winemiller, 2005): both opportunistic and periodic strategists are assumed to be advantageous under relatively high levels of disturbance, though at different levels of scale, and relatively low levels of competitive interactions. Because of their small size, opportunistic species are expected to respond to more stochastic disturbance patterns that manifest in small-scale spatial patches. Periodic species, on the other hand, are expected to respond to more seasonal patterns of disturbance that manifest in large-scale spatial patches. Equilibrium species are predicted to be associated with relatively low levels of disturbance, characterized by fine-grained spatial variability and higher levels of competition.

The basic conceptual model for the analysis is designed to evaluate these predictions, and is both simple and complex at the same time (Figure 4.4). It evaluates the interacting influence of two of the primary factors defined by habitat template theory (Southwood, 1988): a measure of abiotic disturbance (streamflow regime) and biotic interactions, defined by niche breadth (assumed to roughly represent the potential for competitive interactions) in shaping the expression of life-history strategies within local fish assemblages. These factors are, in turn, considered to represent influences across a range of spatial scale. Selected components of flow regime are assumed to reflect both large-scale regional climate factors and network position at the smaller meso-scale (Table 4.1). The potential for biotic interactions is modeled as influenced by both network position and flow regime. The potential for these interactions is quantified for each assemblage by a multivariate measure of species dispersion in habitat space, assumed to be an index of the potential for competitive interactions. The index is based largely on morphological data as surrogates for ecological data (Winemiller, 1991). The basic model is evaluated separately for each life-history strategy, focusing alternately on the influence of selected components of streamflow regime.

In this analysis, flow regime is described by annual patterns of extreme events, specifically variability in peak and low-flow conditions, because they reflect long-term flow characteristics that are presumed linked to large-scale distribution patterns of fish species (Palmer and Poff, 1997). Additionally, extreme flow events can act as important constraints on key life-history characteristics in fishes (Nesler and others, 1988; Naesje and others, 1995; Seegrist and Gard, 1978). Based on this consideration, the focus of the analysis is on streamflow regime as a constraint or limiting factor on the distribution of life-history strategies within fish assemblages. The basic question is whether certain flow conditions, interacting with the potential for biotic interactions, limit or preclude the expression of specific life-history strategies.

This focus requires examination of the limits, i.e. the ceiling or the floor, for the expression of each life-history strategy within an assemblage rather than a measure of central tendency (Konrad and others, 2008). Multivariate measures were utilized to define these limits, based on the tri-lateral life-history model, as follows: (1) Ordination analysis was conducted to describe each life-history strategy based on life-history traits that represent the specific demographic parameters maximized in the model for that strategy (Winemiller and Rose, 1992) (Figure 4.1). The opportunistic and periodic strategies (minimizing generation time and maximizing fecundity, respectively), were assumed to reflect opposing values of the same group of traits, namely growth rate, age at maturity, life span, clutch size, and maximum body size. The equilibrium strategy (maximizing juvenile survival) was assumed to reflect the extent of parental care, ovum size, and clutch size. The tendency of each species toward each strategy was quantified by their ordination scores along the appropriate axis. (2) The boundary or outside limit for the occurrence of each life-history strategy within an assemblage was defined by the extreme value (i.e. the minimum or maximum) of the component species scores observed in the assemblage for the appropriate ordination axis.

It is not possible to utilize standard statistical procedures to evaluate the conceptual model presented here (Figure 4.4), with its interdependence among abiotic and biotic factors and the simultaneous relations of these with influences at the regional and network scale. While this model is relatively simplistic in that it focuses

on a small number of factors certain to be important for fish distribution, it nonetheless represents a complex system of interacting predictor variables. Furthermore, the model provides an opportunity to evaluate a multivariate hypothesis: the occurrence of each fish life-history strategy is constrained by a characteristic interaction of streamflow regime (reflecting influences at the regional and stream network scale) with the potential for competitive interactions. The evaluation of multivariate hypotheses requires a statistical methodology that is suitable for dealing with simultaneous effects among interdependent predictors. Structural equation modeling (SEM) was selected as the statistical method for this study because it is well suited for evaluating multivariate hypotheses where complex interactions exist among predictor variables (Grace, 2006). In contrast to the classic reductionist approach that focuses on single processes in isolation, the SEM approach provides statistical control among predictor variables so that a group of processes can be examined within a single analysis in order to evaluate the relative importance of each. An important corollary is that one can distinguish between direct effects (e.g. flow variability constrains life history) and indirect effects (e.g. flow variability influences the potential for biotic interactions, which in turn is a limiting factor for life history). Moreover, SEM allows the analysis of variables that are specified both as predictors and responses (e.g. flow variability is a product of regional and network factors and a predictor of life history). Finally, SEMs are well suited for evaluating the implications of an *a priori* conceptual model since it must be specified prior to analysis based on the pre-existing and theoretical understanding of the investigator. As a result, a SEM analysis does not seek simply to explain the maximum variance possible but rather to evaluate the specific hypotheses that are described by the model.

The SEM analysis is essentially exploratory in nature, even though it is designed to evaluate (or confirm) the predictions of the conceptual model (Figure 4.3). That is, while multiple models are evaluated—one for each combination of streamflow component and life-history strategy—each model is examined only once. There are insufficient data available for this analysis to allow further testing in a true confirmatory mode with an independent dataset. Additionally, the models are somewhat open-ended in that they merely specify a proposed influence without

defining the specific nature or direction of that influence. Specific hypotheses are embedded in the analysis, nonetheless, based on predictions from the life-history conceptual model (Winemiller, 2005) and habitat template theory (Southwood, 1988) as follows (Figure 4.3B): (1) the opportunistic strategy will be maximized by stochastic streamflow conditions manifesting at relatively small scale, i.e. in small streams where annual peak-flow variability is high, low-flow volume is reduced, and when niche breadth is large or the potential for competitive interactions is low; (2) the periodic strategy will be maximized by highly seasonal large-scale patterns, i.e. in larger streams subject to relatively low variability of annual peak flow, larger volumes at low flow, and when niche breadth is somewhat less large or the potential for competitive interactions is intermediate; (3) the equilibrium strategy will be maximized under relatively stable conditions subject to fine-grained variability, i.e. in the largest streams where flow variability is reduced and low flows are highest, and when niche breadth is small or the potential for competitive interactions is high.

Methods

Study area. This analysis is based on data collected by the U.S. Environmental Protection Agency as part of the Environmental Monitoring and Assessment Program (EMAP), which focused on evaluating ecological conditions in streams within 12 western states (Stoddard and others, 2005). In the upper Missouri River Basin, excluding watersheds with some portion inside Canada, 146 stream reaches were sampled during the summer low-flow season in 2001-2004. Electrofishing or seining the entire channel within the channel reach, defined as 100 times as long as the wetted channel, was conducted to determine fish identification and abundance. For this study, analysis was limited to species presence/absence because it remains fairly constant (in contrast to abundance) over lengthy sampling periods (Matthews and others, 1988; Rahel, 1990; Decker and Erman, 1992). Small tributary streams located less than 16 kilometers from confluence with larger streams (Strahler stream order $\geq$ 6) were omitted from analysis. After additional sub-setting of sites according to species composition (described below), the final dataset included 109 sites (Figure 4.2).

Analysis of streamflow regime. Streamflow metrics to describe the selected components of flow regime were estimated by a regional frequency analysis of streamflow data from gaged sites in the study area (Kelly and Jett, 2006) (Table 4.1). Streamflow data were obtained from the database maintained by the U.S. Geological Survey. Regions, or sets of gaged sites, were defined for each ungaged (EMAP) site based on multivariate analysis of watershed characteristics that were significantly correlated with the relevant streamflow characteristics for gaged sites (Zrinji and Burn, 1994). Separate regional frequency curves for annual peak and 7-day low flows were defined for each ungaged site based on streamflow data from the gaged sites within each site-specific region. These curves were scaled by the appropriate index flow, i.e. mean annual peak or 7-day low-flow value, so they defined a dimensionless frequency distribution (Hosking and Wallis, 1993). Specific quantiles, such as the 2-year or 100-year flow, were determined directly from the regional curve for each ungaged site. The magnitude of 7-day 10-year low-flow was computed by multiplying the 10-year quantile by the index flow (mean annual 7-day low flow, estimated by regression against watershed and climate characteristics). See Kelly and Jett (2006) for further details on this analysis.

Analysis of life-history and morphological traits. Only native and common fish species were selected for analysis. Common species were defined operationally as comprising at least 5 percent of the relative abundance contributing to the numerical total for a site. This strategy was intended to exclude transient species that were assumed to have negligible interaction with the core assemblage structure. Additionally, species were excluded if they were observed at fewer than 3 sites. The final N was 29 species from 10 families (Table 4.2).

Life-history traits were selected to describe the primary dimensions of the trilateral life-history model as comprehensively as possible with the available data (Table 4.3). These included measures of growth rate (Bertalanffy growth coefficient), age at maturity, life span, mean clutch size, maximum size (length), mean ovum size, and a measure of parental care. The extent of parental care was coded by a progressively increasing index determined from reproductive guild classifications defined by Balon (1975) as follows: pelagophil = 11; lithopelagophil = 12; lithophil =

13; phytolithophil = 14; phytophil = 15; lithophil brood hider = 23; nest guarder = 25; speleophil = 27.

Morphological data were chosen as surrogates for habitat association based on established relationships between form and function in fishes (Gatz, 1981; Winemiller, 1991) and augmented by data to describe trophic level (Table 4.3). These included measures to describe relative body depth (maximum body depth / standard length), relative length of the caudal peduncle (peduncle length / standard length), an index of ventral flattening (proportion of body depth below the midline at the point of maximum depth), and the position of the eye (proportion of head depth occurring below the middle of the eye). These are presumed to reflect habitat utilization as follows: body depth is expected to be maximized when water velocity is low; the caudal peduncle length is expected to be maximized in strong swimmers and when water velocity is high; ventral flattening is expected to be associated with benthic fishes; and the position of the eye reflects the distinction between benthic fishes (dorsal placement) versus nektonic fishes (lateral placement). Trophic position was quantified as the rank of the species in the food web, estimated by 1 + the mean trophic level of characteristic food items (weighted by their contribution) based on data from the literature.

Data to represent most life-history traits and trophic-level data were acquired from FishBase, a web database maintained by the World Fish Center (Froese and Pauly, 2007). Additional data were obtained from the Depository of Unpublished Data, CISTI, National Research Council of Canada (Winemiller and Rose, 1992). Morphological data were determined from measurements of museum specimens at the Division of Ichthyology, Natural History Museum and Biodiversity Research Center of the University of Kansas. Specimens for measurement were selected from samples collected as near as possible to the center of their range within the study area. Measurements were taken with vernier calipers to the nearest 0.1 mm (< 130 mm), and to the nearest 1 mm with a ruler (> 130 mm), according to methods described in Winemiller (1991). Three specimens of adult size were measured for each species, with values expressed as the mean.

Statistical analysis. Scores to determine the association of species with each of the three life-history strategies were based on principal component analysis of Euclidian distances between selected trait values, first normalized by the maximum for each trait. The traits to define each life-history strategy were specified as follows (Table 4.3): The opportunistic and periodic strategies were identified by an ordination defined by Bertalanffy growth coefficient, age at maturity, life span, clutch size, and maximum length. The equilibrium strategy was identified by ordination of clutch size, ovum size, and the extent of parental care. The significance of each component was evaluated by the size of the eigenvalue in two ways: (1) if the eigenvalue > 1, it was considered to contain more information than individual observed variables (Tabachnick and Fidell, 2001); and (2) by the broken-stick model, so that the component was considered statistically significant when the observed eigenvalue exceeded the broken-stick eigenvalue (McCune and Grace, 2002). Interpretation of the ordination results was based on the correlations (Pearson's r) between the ordination scores and the individual variables used to construct the ordinations.

Multivariate analysis of morphological and trophic-level data (Table 4.3) was conducted to provide a measure of the niche breadth or potential for competitive interactions within each assemblage. The measure of niche breadth, or species dispersion in morphological space, was considered a surrogate for the lack of similarity of co-occurring species along multiple dimensions of habitat and resource use (Winemiller, 1991), and therefore an inverse measure of the potential for competition between them. All data were first standardized to fit the normal distribution by subtracting the mean and dividing by the standard deviation. Multivariate Euclidian distances were computed for each species pair, and nearest (or minimum) neighbor distances (NND) were determined for all species co-occurring within each assemblage. Mean NND values, then, were utilized to represent the aggregate niche breadth, or competitive potential, for each assemblage.

SEM models were constructed for each of two components of flow regime: peak-flow variability and low-flow volume, where measured variables replaced the general variables described in the general conceptual model (Table 4.1). Although SEM models represent a set of simultaneous equations, results are presented as visual

graphs that depict the structure and interconnections proposed by the model. For this analysis, these models include both independent variables, termed exogenous because they originate outside the model, and dependent or response variables, termed endogenous because are dependent upon influences described by the model. Endogenous variables are defined as latent variables that are measured indirectly by measured variables. For example, the latent variable "peak-flow variability" was measured by variability in peak-flow magnitude and in peak-flow timing (Table 4.1). Low-flow volume was measured by a single variable (7-day 10-year low flow magnitude) and niche breadth was measured by mean NND.

As described by the model, the relationships between variables may include both direct and indirect effects. The direct effect of one variable on another is one that is explained completely by the relationship between them. An indirect effect represents the effect of one variable on another through mediation by a third. It is described by a compound effect equal to the product of the path coefficients connecting the predictor and response variables. For example, the indirect effect of flow regime on life history is equal to the effect of flow regime on niche breadth multiplied by the effect of niche breadth on life-history strategy (Figure 4.4). The total effect is measured as the sum of direct and indirect effects, and is commonly measured as the simple correlation between them. The ability to evaluate the direct and indirect contributions to the total effect of one variable on another provides an important strength of the SEM approach.

The initial step in model building was to determine which of the regional variables explained significant and unique variance in each flow component. Once satisfactory models were obtained for flow components, the final models were constructed to include niche breadth and life-history strategies (Figure 4.5). Each of the flow models were then evaluated separately for each of the three life-history strategies, making a final total of six models. Variables were transformed as necessary before analysis.

Maximum likelihood estimation was used to evaluate the models. Because SEM models propose relationships that generate a characteristic covariance structure, the models are tested by comparing the model covariance structure with that generated

by the measured data. Chi-square statistics and associated *p* values describe the consistency of the data with the model: a non-significant chi-square ($p>.05$) indicates that no difference can be observed between the two. Another index of fit is the root mean square error of approximation (RMSEA), which indicates a reasonable fit in relation to the degrees of freedom in the model. Generally, RMSEA < .05 -.08 suggests a close to reasonably close model fit although the criterion is a subjective one (Browne and Cudeck, 1993). Best-fitting models were developed to maximize fit according to these indices; pathways and variables were only included in the final models if they corresponded with unique variance explained for at least one life-history strategy and resulted in worse models if they were excluded. Analyses were based on actual covariances, not correlations, although the reported path coefficients are standardized in the figures for ease of interpretation. Chi-square statistics and RMSEA values are also presented for the final models.

Results

       <u>Life-history strategies</u> Principal component analysis of life-history traits indicated a clear separation of species along the primary opportunistic-periodic (O-P) axis defined by growth rate, age at maturity, life span, clutch size, and maximum size (Figure 4.6A). The first principal component was significant and clearly dominant, explaining approximately 78 percent of the total variance (Table 4.4). Species tending toward the endpoint of the opportunistic strategy were characterized by fast growth (as measured by Bertalanffy growth coefficients), early age at maturity, short life span, small clutch size, and small size (as measured by maximum length) (Figure 4.6A). Those tending toward the periodic strategy showed the opposite characteristics. Because it captured all of the important features that characterize the opportunistic and periodic life-history strategies, the scores along the first O-P component were utilized to score each species according to their tendency toward each strategy. The most positive scores along this axis indicate the strongest opportunistic tendency, and the most negative scores indicate the strongest periodic tendency. The distribution of fish families along this axis indicated that the most opportunistic species were from the family Cyprinidae, while the most periodic species were members of the families Catostomidae, Esocidae, and Hiodontidae.

The analysis of traits most related to the equilibrium strategy was not as clear cut, possibly reflecting the small number of variables that were available to describe the equilibrium strategy. The eigenvalues for both of the first two principal components exceeded 1, though just barely, indicating that each component contained at least minimally more information than the individual variables (Table 4.4). The first component showed a clear separation between clutch size and the extent of parental care (explaining 47 percent of the total variance), while the second showed the additional influence of ovum size (explaining another 36 percent) (Figure 4.6B). Although the cumulative variance explained by both components was 84 percent, neither was statistically significant based on comparison with the broken-stick eigenvalue. To utilize the maximum information from this analysis, the scores along both of the first two components (E) were summed to quantify the tendency toward equilibrium strategy. The distribution of fish families along these two axes shows that the species with the strongest equilibrium characteristics were members of the families Ictaluridae and Salmonidae.

In constructing the SEM models to evaluate the constraints or limits on the expression of life-history strategies within fish assemblages, limits for each assemblage were defined by the extreme values of scores along the appropriate axis. The tendency toward the opportunistic strategy was quantified by the maximum score for each assemblage along the O-P axis. Those assemblages with high scores along this axis contained at least one species that showed a strong tendency toward the opportunistic life-history strategy. The strength of the tendency toward the periodic strategy was quantified by the minimum score for each assemblage along the O-P axis. Because this score is a negative value for strongly periodic species, it was first multiplied by -1 to measure the periodic tendency directly. As a result, assemblages with the highest scores along this axis contained at least one species that strongly manifested the periodic strategy. Similarly, the tendency toward the equilibrium strategy was quantified by the maximum score along the E axis.

SEM results Models were considered to be significant when *p* values associated with the chi-square fit indices exceeded .05, indicating that no statistically significant difference was detected between the covariance structures predicted by the

model and observed in the data. Based on this criterion, all models relating streamflow components to the distribution of opportunistic and periodic life-history strategies were found to be significant (Figures 7-8). The chi-square indices were roughly corroborated by the RMSEA values for these models as well, which ranged between .029 and .080. The explanation of variance (R^2) was moderate, equaling .36 and .34 for the opportunistic strategy and .27 and .29 for the periodic strategy. The same results were not observed for the equilibrium strategy (Figure 4.9), where the model for peak-flow variability did not adequately fit the data (p=.004, RMSEA=.121) and the model for low-flow volume was only marginally significant (p=.092, RMSEA=.096). The R^2 value for the low-flow model was low (.15).

Aggregate niche breadth in morphological space was observed in all models to be positively associated with peak-flow variability and low-flow volume (Figure 4.7-4.9). Because this measure provides an inverse measure of the potential for competitive interactions, small niche breadth represents assemblages of relatively similar species and correspondingly high competitive potential. Large niche breadth represents assemblages of relatively dissimilar species (i.e. low competitive potential). These results suggest that species were more different from one another relative to habitat utilization, i.e. the potential for competition within an assemblage was relatively low, when peak-flow variability was high and when low-flow volume was high.

Examining the models in more detail, the opportunistic strategy was positively related to variability in peak flow but inversely related to low-flow volume (Figure 4.7 and 4.10) (Table 4.5). This means that assemblages containing species that were more opportunistic were associated with higher levels of flow variability. Conversely, those assemblages associated with larger values of low-flow volume were comprised of species that were relatively less opportunistic. The association of the opportunistic strategy and niche breadth was consistently positive across all models, indicating that assemblages where niche breadth was large (or competitive potential was low) contained species that were more opportunistic in character. These results are consistent with the predictions of the first hypothesis: the opportunistic strategy will

be maximized when flow variability is high, when low-flow volume is low, and when niche breadth is large or the potential for competition is low.

The model results presented in Figure 4.7 describe direct effects between predictors and responses; because of the interaction of flow components with competitive potential, however, the total effect of those components on life history differs in some models from the direct effect shown. For example, the total effect of peak-flow variability on the opportunistic strategy is actually larger than the direct effect because it incorporates the indirect effect mediated by the potential for competition (Table 4.5). In other words, the model describes a complex interaction of peak-flow variability with competitive potential in strengthening the expression of the opportunistic life-history strategy, whereby flow variability was associated with increased opportunistic character both directly and indirectly. In the terms of the model, the indirect effect was mediated through suppression of the potential for competition, thereby reducing its negative impact on the opportunistic strategy. The opposite pattern was observed for low-flow volume, where the total effect was comprised of a negative direct effect that was partially reversed by the positive indirect effect via competitive potential (Table 4.5). This implies even greater complexity in the effect of low-flow volume on the distribution of opportunistic strategists—directly constraining them on the one hand, while at the same time lessening the potential for competitive interactions, which indirectly reduces the apparent inhibition of opportunistic species.

Finally, as defined by the proposed models, regional and network factors had only indirect effects on life history, mediated through their association with streamflow regime and/or competitive potential. Regional climate factors were strongly associated with patterns of peak-flow variability, while stream order showed only a small effect. In contrast, low-flow volume was predominantly related to stream order and less affected by regional factors. Results indicated that the opportunistic strategy was moderately responsive to large-scale regional factors, i.e. opportunistic character was more pronounced where precipitation intensity was high and less pronounced under conditions of increased annual precipitation (Table 4.5). Additionally, the opportunistic strategy was positively associated with stream order

(all other factors being equal), implying that larger streams were observed to contain species with relatively stronger opportunistic character.

The periodic strategy showed the opposite relationship with flow, though somewhat weaker, being less pronounced when peak-flow variability was high and more pronounced at higher low-flow volume (Figures 8 and 10). The only similarity between the responses of these two strategies was a negative association with the potential for competition. Assemblages where species were ecologically more distinct, with reduced potential for competitive interactions, showed a stronger periodic life-history character. The interplay of direct and indirect effects also shows a complex pattern of relationships among factors related to the periodic strategy. The indirect effect of peak-flow variability on the periodic strategy was mediated by a decrease in potential competitive interactions. As a result, the indirect effect was positive so that the total effect was less negative than the direct effect (Table 4.5). In fact, the total effect was close to nil, implying that peak-flow variability did not constrain the occurrence of the periodic strategy. Similarly, the total effect of low-flow volume was larger than the direct effect because of the positive influence mediated through competitive potential. In contrast with the opportunistic strategy, the periodic strategy showed very little response to regional factors (Table 4.5). The strongest association was with stream order, indicating that periodic strategists were significantly more likely to be observed in larger streams. These results largely confirm the predictions for flow components in the second hypothesis, although they contradict the prediction that the periodic strategy would be maximized when competitive interactions were relatively high.

Though results for the equilibrium strategy were limited because neither model was strongly significant ($p<.05$), they suggest that the predictions of the third hypothesis were largely not corroborated (Figure 4.9 and 4.10). The model for peak-flow variability was not consistent with the data, indicating the model could not explain the distribution of the equilibrium strategy. These results imply that regional climate factors were not important relative to the distribution of the equilibrium strategy. The second model was marginally significant, and indicated a very small effect of low-flow volume, essentially no influence on the occurrence of the

equilibrium strategy. Stream order showed a small but positive influence (Table 4.5). The only strong effect was observed for niche breadth, which was positively associated with the equilibrium strategy. In other words, sites where the potential for competition was high were less likely to be associated with species with increased tendency toward the equilibrium life-history strategy.

Examining the interplay of direct and indirect effects for the low-flow model indicates that the indirect effect of low-flow volume on the equilibrium strategists mediated through the suppression of competitive potential essentially reversed the direct effect (Table 4.5). Because the total effect of low-flow volume was barely positive, though close to zero, these results are marginally consistent with the prediction of the third hypothesis that the equilibrium strategy will be exhibited when flow conditions are relatively stable. Regardless, they are clearly contrary to the prediction that the equilibrium strategy is more likely to be associated with high levels of competitive interactions.

Discussion

Because of the relatively close association between fish families and the endpoints of each life-history strategy depicted in Figure 4.6, this analysis essentially evaluates the constraints on the distribution of three to six families within the upper Missouri River Basin. The designation of life-history strategy as defined in this study closely coincides with the characteristics of the families that most strongly represent each strategy. Species tending most strongly toward the opportunistic strategy were largely from the family Cyprinidae, which contains many species known as "pioneers" or colonizing species. Cyprinid species are also very common prey fishes, subject to high predation pressure. They are dominated by fast growing, small-bodied fishes that often reach maturity in a single year. Those exhibiting the strongest periodic character were primarily from the family Catostomidae, widely recognized for their seasonal spawning migrations, and included single species from Esocidae and Hiodontidae that also migrate to specific areas for spawning. These fishes are relatively long-lived, large-bodied and broadcast large numbers of eggs in mass spawning events. The equilibrium strategy was most strongly associated with members of the family Ictaluridae, as well as a single species from Salmonidae. Ictalurid, or catfish species

spawn in cavities and guard their young, while salmonids build nests or redds before depositing their eggs.

Looking at total effects, SEM results indicate that opportunistic species were strongly responsive to peak-flow variability, which exhibits a large-scale regional pattern across the study area. High-elevation snowmelt streams in the west show a characteristically low variability in peak flow magnitude and timing, while lowland streams show much greater variability in peak regime from year to year. These patterns are closely associated with large-scale climate patterns that determine annual precipitation volume and rainfall intensity. Distribution patterns for opportunistic species validate theoretical habitat template predictions as a clear response to streamflow disturbance. Nonetheless, my results indicate that the influence of temporal stochasticity is mediated in this study area primarily by large-scale rather than small-scale variability. In terms of constraints, these results suggest that opportunistic species may be partially limited by large-scale factors related to climate (which are also associated with topography). Regional climate patterns apparently serve as effective constraints on the expression of the opportunistic life-history strategy via their impact on flow regime, thereby excluding those species from upland streams where flow variability is low. Opportunistic species also show an additional response to factors at the network scale, with a stronger tendency to occur in larger streams. These results are consistent with the very strong negative response of these species to the potential for competitive interactions as measured in this study, which is reduced in larger streams.

In contrast, the most periodic species showed little constraint by large-scale or regional factors on their distribution but were most responsive to influences at the scale of stream order. The expectation was that these species would be associated with more predictable (i.e. less variable) patterns of peak flow, which was observed even though the total effect of peak-flow variability was low. The families that most strongly exhibit the periodic strategy were widely distributed in lowland streams throughout the study area, and therefore occur in conditions where peak-flow variability is high. The presumed requirement of these periodic species for highly seasonal and relatively predictable flow conditions may be partially realized by their

strong tendency toward larger order streams with higher volume at low flow. For these fishes, it may also be that large body size, a long life span, and the characteristic habit of spawning migration are key attributes for survival on the Great Plains. Life spans much greater than one year mean periodic species are less vulnerable to flow variability at the annual scale, and the habit of spawning migration implies that spatial variability at the network scale may be most important. Because the periodic strategy is essentially bet-hedging, where large numbers of eggs are released into variable environments over sufficient time in order to ensure that some will survive, it is a viable strategy for dealing with high levels of spatial variability (Partridge and Harvey, 1988).

Understanding the factors related to the distribution of the equilibrium strategy is complicated because of the large differences between the two families that most strongly represent this strategy in this study. The lack of a significant model for peak-flow variability is not surprising because the dominant equilibrium strategists were distributed across the full range of peak-flow regime in the study area: catfish are characteristic species in lowland streams, subject to high levels of peak-flow variability, while salmonids are found in mountain streams where peak-flow variability is low. Even regarding low-flow volume, despite the marginal significance of the model, the relationship of flow with the equilibrium strategy was unclear and essentially nil. Again, these results reflect the diversity of streams where equilibrium species occur: catfish in large lowland streams and salmonids in small headwater streams. The diversity of stream conditions is reflected in the species themselves, especially related to stress tolerance: catfish are well adapted to tolerate adverse conditions (i.e. high water temperature and low concentrations of dissolved oxygen) while salmonids are very sensitive to adverse conditions. It is likely that these two groups of fishes represent two distinctly different kinds of equilibrium species: salmonids, adapted to relatively stable flow conditions and catfish, adapted to adverse conditions independent of flow.

The equilibrium strategy is proposed by the life-history model to maximize juvenile survival under density dependent conditions largely driven by resource limitation (Winemiller and Rose, 1992). Nonetheless, the most significant factor

related to the distribution of the equilibrium strategy that emerges from this analysis is the strong negative relationship with the potential for competitive interactions. This result is disconcerting because it confounds the prediction that the equilibrium strategy would be advantageous under conditions of high competitive pressure. A partial explanation may be found in the ambiguous nature of the measure used to describe competitive potential. The potential for competitive interactions was measured by the inverse of niche breadth as measured by the NND index, which quantifies the aggregate similarity of all component species observed within a sample reach. This assemblage-scale measure assumes that co-occurrence of species that are similar to one another is associated with high levels of competition between those species for habitat and food resources. It contains no information about how similar species may segregate from each other along micro-habitat gradients within the reach, thereby reducing competitive interactions among them. It is also a somewhat confusing measure, since it presumes that competitive potential can be measured simply by co-occurrence patterns of similar species in present time, providing no consideration of how competition in the past may have structured those patterns so that similar species no longer co-occur (Connell, 1980). In this way, the intensity of competition in the present is equated with the importance of competition in structuring the assemblage, which confuses the process of competition with the product of competition (Weldon and Slauson, 1986).

These considerations provide the basis for speculation about the observed relation between competitive potential and the distribution of the equilibrium strategy, especially because it is predicted that this strategy would be associated with the highest competitive ability. As mentioned, in this study the equilibrium strategy was most pronounced in fishes from two families, Ictaluridae and Salmonidae, which occur in very different kinds of streams. Ictalurid or catfish species were largely observed in large lowland rivers, which were generally associated with larger niche breadth or lower levels of potential competitive interactions. This result may be due simply to the greater complexity of habitat available so that large numbers of dissimilar species can co-occur. Salmonids were concentrated in streams at high elevation, where niche breadth was large because the fish assemblage was often comprised of only one or two

very dissimilar species. Again, this result may be due simply to the limited number of species adapted to cold water mountain conditions. Or, the reduced level of competitive potential between co-occurring species under both these scenarios may be a consequence of past competitive pressure that resulted in segregation of similar species on a scale larger than the reach sampled in this study. The issue cannot be resolved with the current data.

In general, the proposed conceptual model, the multivariate hypothesis based on habitat template theory, was confirmed for the opportunistic and periodic life-history strategies: characteristic associations with streamflow regime and competitive potential were observed (Figure 4.11). Species associated with both of these strategies showed significant tendencies related to streamflow regime, which were consistent with the predictions of habitat template theory although at different spatial scales than originally presumed. Still, despite the negative direct relationship with peak-flow variability, the periodic strategy is clearly successful under conditions of high flow variability. Because streamflow variability is often considered to be an important component of disturbance for stream species, these results confirm that opportunistic and periodic fishes are roughly comparable to the classic *r*-selected species (*sensu* Southwood, 1977), as has been noted by others (Olden and others, 2006). Both the opportunistic and periodic strategies apparently provide relatively flexible strategies for dealing with high levels of environmental variability.

These results demonstrate that small, short-lived species can be strongly influenced by large-scale patterns of streamflow variability while large, long-lived species may respond only weakly to the same influences. In this study, both these groups of species show similar distribution patterns, largely confined to lowland streams. Nonetheless, SEM results suggest the level of constraint by flow regime differs for each strategy, representing a complex interaction between the scale of variability and life span of the species. Because opportunistic species are small and short-lived, they respond strongly to regional factors that correspond with strong patterns of annual streamflow variability. Periodic species, on the other hand, are large and long-lived and therefore not affected in the same way by annual flow

variability. The periodic strategy is apparently more responsive to spatial variability within the meso-scale of the stream network.

The general conceptual model was not confirmed for the equilibrium life-history strategy, as the SEM models either reflected limited correspondence with the data or showed that flow had little explanatory power. Results indicate that the equilibrium strategy was exhibited with no regard to flow disturbance (Figure 4.11), occurring in streams across the full range of peak-flow variability. Contrary to expectation, this strategy also showed a tendency toward a reduced potential for competitive interactions. It is likely that these results reflect the versatility of the equilibrium strategy in dealing with both stability and adversity.

References

Balon, E.K., 1975. Reproductive guilds of fishes: a proposal and definition. Journal of the Fisheries Research Board of Canada 32: 821-864.

Biggs, B.J.F., V.I. Nikora, and T.H. Snelder, 2004. Linking scales of flow variability to lotic ecosystem structure and structure. River Research and Applications 21: 283-298.

Connell, J.H., 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35(2): 131-138.

Decker, L.M. and D.C. Erman, 1992. Short-term seasonal changes in composition and abundance of fish in Sagehen Creek, California. Transactions of the American Fisheries Society 121: 297-306.

Diez, J.M. and H.R. Pulliam, 2007. Hierarchical analysis of species distributions and abundance across environmental gradients. Ecology 88(12): 3144-3152.

Dodds, W.K., K. Gido, M.R. Whiles, K.M. Fritz, and W.J. Matthews, 2004. Life on the edge: the ecology of Great Plains prairie streams. BioScience 54(3): 205-216.

Fausch, K.D., C.E. Torgersen, C.V. Baxter, and H.W. Li, 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52(6): 483-498.

Froese, R. and D. Pauly, 2007. Editors, FishBase: World Wide Web electronic publication (www.fishbase.org).

Gatz, A.J. Jr. 1981. Morphologically inferred niche differentiation in stream fishes. American Midland Naturalist 106: 10-21.

Grace, J.B., 2006. Structural equation modeling and the study of natural systems. Cambridge University Press.

Hosking, J.R.M. and J.R. Wallis, 1993. Some statistics useful in regional frequency analysis. Water Resources Research 29(2): 271-281.

Kelly, V.J. and S.M. Jett, 2006. Ecologically relevant quantification of streamflow regimes in western streams. EPA/620/R-06/056, U.S. Environmental Protection Agency, Washington DC.

Konrad, C.P., A.M.D. Brasher, and J.T. May, 2008. Assessing streamflow characteristics as limiting factors on benthic invertebrate assemblages in streams across the western Unites States. Freshwater Biology 53: 1983-1998.

Levin, S.A., 1992. The problem of pattern and scale in ecology. Ecology 73: 1943-1967.

MacArthur, R.H., 1975. The theory of the niche. Pages 159-176 *in* Population Biology and Evolution (Lewontin, R., ed). Syracuse University Press.

Matthews, W.JU., R.C. Cashner, and F.P. Gelwick, 1988. Stability and persistence of fish faunas and assemblages in three Midwestern streams. Copeia 1988: 947-957.

McCune, B, and J.B.Grace, 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR.

Naesje, T., B. Jonsson, J. Skurdal, 1995. Spring flood: a primary cue for hatching of river spawning Coregoninae. Canadian Journal of Fisheries and Aquatic Sciences 52: 2190-2196.

Nesler, T.P., R. Muth, A.F. Wasowicz, 1988. Evidence for baseline flow spikes as spawning cues for Colorado squawfish in the Yampa River, Colorado. American Fisheries Society Symposium 5: 68-79.

Olden, J.D., N.L. Poff, K.R. Bestgen, 2006. Life-history strategies predict fish invasions and extirpations in the Colorado River basin. Ecological Monographs 76(1): 25-40.

Palmer, M.A. and N.L. Poff, 1997. Heterogeneity in streams. Journal of the North American Benthological Society 16: 169-173.

Partridge, L. and P.H. Harvey, 1988. The ecological context of life history evolution. Science 241(4872): 1499-1455.

Peckarsky, B.L., 1983. Biotic interactions or abiotic limitations? A model of lotic community structure. Pages 303-323 *in* Dynamics of lotic ecosystems (T.D. Fontaine and S.M. Bartell, eds). Ann Arbor Science, Ann Arbor, MI.

Poff, N.L., 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of North American Benthological Society 16: 391-409.

Poff, N.L. and J.V. Ward, 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Canadian Journal of Fisheries and Aquatic Sciences 46: 1805-1818.

Rahel, F.J., 1990. The hierarchical nature of community persistence: a problem of scale. The American Naturalist 136: 328-344.

Reice, S.E., R.C. Wissmar, and R.J. Naiman, 1990. Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. Environmental Management 14(5): 647-659.

Resh, V.H., A.V. Brown, A.P. Covich, M.E. Gurtz, H.W. Li, G.W. Minshall, S.R. Reice, A.L. Sheldon, J.B. Wallace, and R.C. Wissmar, 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7(4): 433-455.

Schlosser, I.J., 1991. Stream fish ecology: a landscape perspective. BioScience 41: 704-712.

Seegrist, D.W. and R. Gard, 1972. Effects of floods on trout in Sagehen Creek, California. Transactions of the American Fisheries Society 101: 478-482.

Southwood, T.R.E., 1977. Habitat, the templet for ecological strategies? The Journal of Animal Ecology 46(2): 336-365.

- 1988. Tactics, strategies and templets. Oikos 52: 3-18.

Statzner, B., J.A. Gore, and V.H. Resh, 1988. Hydraulic stream ecology: observed patterns and potential applications. Journal of North American Benthological Society 7: 307-360.

Stearns, S.C., 1976. Life-history tactics: a review of the ideas. The Quarterly Review of Biology 51(1): 3-47.

Stoddard, J.L., D.V. Peck, S.G. Paulsen, J. Van Sickle, C.P. Hawkins, A.T. Herlihy, R.M. Hughes, P.R. Kaufmann, D.P. Larsen, G. Lomnicky, A.R. Olsen, S.A. Peterson, P.L. Ringold, and T.R. Whittier, 2005. An ecological assessment of western streams and rivers. EPA 620/R-05/005, U.S. Environmental Protection Agency, Washington DC.

Tabachnich, B.G. and L.S. Fidell, 2000. Using multivariate statistics, 4th edition. Allyn and Bacon, Needham Heights, MA.

Tilman, D., 1976. Ecological competition between algae: experimental confirmation of resource-based competition theory. Science 192: 463-465.

Weldon, C.W. and W.L. Slauson, 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. The Quarterly Review of Biology 61(1): 23-44.

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

Winemiller, K.O., 1991. Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. Ecological Monographs 61(4): 343-365.

- 2005. Life history strategies, population regulation, and implications for fisheries management. Canadian Journal of Fisheries and Aquatic Sciences 62: 872-885.

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

Winston, M.R., 1995. Co-occurrence of morphologically similar species of stream fishes. The American Naturalist 145(4) 527-545.

Zrinji, Z. and D.H. Burn, 1994. Flood frequency analysis for ungaged sites using a region of influence approach. Journal of Hydrology 153: 1-21.

Table 4. 1. Variables used in the basic models examined in this study.

Variable, by category	Abbreviation	Description
Regional		
Precipitation intensity	P10006	100-year 6-hour precipitation, at site
Annual precipitation	precip_m	Approximate annual precipitation
Stream density	density	Stream length / watershed area
Stream network		
Stream order	order	Strahler stream order
Components of streamflow regime		
Variability in peak-flow magnitude	disp	Difference between 100-year and 2-year peak flow (normalized by mean annual peak flow)
Variability in peak-flow timing	fjdcv	Coefficient of variation for timing of annual peak flow (mean annual Julian day)
Low-flow volume	log_flow	Logarithm of 10-year 7-day low flow magnitude
Potential for competitive interactions		
Niche breadth	morpho_nnd2	Mean nearest-neighbor multivariate distance between species for fish assemblages, based on morphology and trophic level
Life-history strategy		
Opportunistic	max_op	Maximum value within each assemblage for species scores along PCA axis defined by k, tm life, lm, and clutch
Periodic	min_op	Minimum value within each assemblage for species scores along PCA axis defined by k, tm life, lm, and clutch
Equilibrium	max_e	Maximum value within each assemblage for species scores along 2 PCA axes defined by clutch, ovum and parent

Table 4. 2. Selected species and life-history traits.
[see Table 4.3 for definition of traits]

Family	Scientific name	k	Life	Lm	Tm	Log-clutch	ovum	parent
Catostomidae	*Carpiodes carpio*	0.11	26.0	36.1	5.9	5.0	1.5	12
	C. cyprinus	.11	26.0	37.1	5.9	4.6	1.4	12
	Catostomus catostomus	.11	26.2	36.1	6.1	4.2	2.9	12
	C. commersonii	.15	19.0	30.8	4.4	4.8	3.2	12
	C. platyrhynchus	.28	10.1	14.2	2.7	3.4	1.8	13
	Moxostoma macrolepidotum	.10	28.7	41.5	6.3	4.3	1.9	13
Centrarchidae	*Lepomis cyanellus*	.36	7.9	19	2.0	4.5	1.2	25
	L. humilis	.50	5.6	10	1.6	3.1	0.5	25
Cottidae	*Cottus bairdii*	.18	15.5	10	4.4	2.3	2.0	25
Cyprinidae	*Cyprinella lutrensis*	.81	3.4	6.4	1.1	2.9	1.2	25
	Hybognathus argyritis	.62	4.5	8.2	1.3	2.9	1.0	11
	H. placitus	.57	4.9	8.8	1.4	2.9	1.2	11
	Luxilus cornutus	.42	6.7	11.8	1.9	3.1	1.5	23
	Notropis atherinoides	.87	3.2	7.3	1.0	2.5	1.0	11
	N. dorsalis	.90	3.1	5.8	1.0	2.5	1.0	25
	N. stramineus	.89	3.1	5.8	1.0	2.5	0.70	14
	Pimephales promelas	.73	3.8	7.0	1.2	2.6	1.3	25
	Platygobio gracilis	.25	11.4	19.6	2.9	3.7	1.2	11
	Rhinichthys cataractae	.26	11	14.3	3.0	2.7	1.0	23
	Semotilus atromaculatus	.26	10.9	18.5	2.8	3.6	1.0	23
Esocidae	*Esox lucius*	.12	23.4	59.7	5.1	4.5	2.8	15
Hiodontidae	*Hiodon alosoides*	.12	23.7	27.1	5.6	4.2	4.0	12
Ictaluridae	*Ameiurus melas*	.27	10.6	37.1	2.4	3.5	3.0	27
	Ictalurus punctatus	.24	12.1	68.5	2.5	3.9	3.8	27
	Noturus flavus	.54	5.3	19.0	1.3	2.3	3.8	27
Percidae	*Sander vitreum*	.22	13.1	42.7	2.9	4.9	1.8	12
Salmonidae	*Onchorhynchus clarki*	.32	9.1	53.1	2.0	3.2	4.7	23
	Prosopium williamsoni	.20	14.3	39.1	3.2	3.7	3.7	13
Sciaenidae	*Aplodinotus grunniens*	.23	12.5	51.2	2.7	5.4	1.4	11

Table 4. 3. Definition of life-history and morphological traits.

Life-history traits		
k	Bertalanffy k [1]	Rate (1/year) at which the asymptotic length is approached, based on $L_t = L_\infty (1 - e^{-k(t-t_0)})$ where L_t is the length at age t, L_∞ is the asymptotic length of the individual, and k is the von Bertalanffy growth rate
life	Life span [1]	Approximate maximum age (years), calculated as the age at 95% of L_∞
Lm	Maximum length [1]	Maximum total length (cm) ever reported for the species in question
Tm	Age at maturity [1]	Mean age (years) at which fish of a given population mature for the first time, calculated from the length at first maturity using the inverse of the von Bertalanffy growth function
clutch	Clutch size [2]	Mean batch fecundity for a local population, based the sum of number of individuals in an age or size class times the number of mature eggs per clutch for that class, divided by the number of classes in the population
ovum	Ovum size [2]	Mean diameter of mature (fully yolked) ovarian oocytes (to nearest 0.01 mm)
parent	Extent of parental care [3]	Parental care coded by classes proposed by Balon (1975) (see text for details)
Ecological and morphological traits		
Trophic level [1]		Rank of the species in a food web, estimated as 1 + mean trophic level of food items (weighted by the contribution of the various food items)
Body depth [4]		Maximum body depth / standard length
Peduncle length [4]		Caudal peduncle length / standard length
Ventral flattening [4]		Proportion of body depth below the midline at the point of maximum depth
Eye position [4]		Proportion of head depth at the middle of the eye, occurring below the middle of the eye
[1] FishBase, Froese and Pauly, 1998; [2] CISTI, Winemiller and Rose, 1992; [3] unpublished EMAP data [4] Measurements from KU Museum; see text for explanation of data sources		

Table 4. 4. Results from principal component analysis of life-history traits.

	PCA axis	
Opportunistic-periodic strategy	1	2
Eigenvalue	3.88	.64
Proportion of variation	77.7	12.8
Cumulative variation	77.7	90.5
Equilibrium strategy		
Eigenvalue	1.42	47.5
Proportion of variation	1.09	36.3
Cumulative variation	47.5	83.7

Table 4. 5. Standardized total, direct, and indirect effects of predictors as constraints on life-history strategies. [for models in Figure 4.4]

Model predictor	Total	Direct	Indirect
Opportunistic life-history strategy			
Streamflow components			
Peak-flow variability	.327	.243	.084
Low-flow volume	-.143	-.253	.110
Inverse potential for competitive interactions			
Niche breadth	.556 to .711	556 to .711	0
Regional factors			
Precipitation intensity	.217	0	.221
Annual precipitation	-.162	0	-.165
Stream density	.049	0	.049
Network factor			
Stream order	.177 to .214	0	.177 to .214
Periodic life-history strategy			
Streamflow components			
Peak-flow variability	-.052	-.139	.087
Low-flow volume	.245	.163	.082
Inverse potential for competitive interactions			
Niche breadth	.507 to .598	.507 to .598	0
Regional factors			
Precipitation intensity	-.035	0	.035
Annual precipitation	.026	0	-.026
Stream density	-.085	0	-.085
Network factor			
Stream order	.276 to .341	0	.276 to .341
Equilibrium life-history strategy			
Streamflow components			
Peak-flow variability	n.s.	n.s.	n.s.
Low-flow volume	.037	-.034	.071
Inverse potential for competitive interactions			
Niche breadth	.421	.421	0
Regional factors			
Precipitation intensity	n.s.	n.s.	n.s.
Annual precipitation	n.s.	n.s.	n.s.
Stream density	-.013	0	-.013
Network factor			
Stream order	.173	0	.173

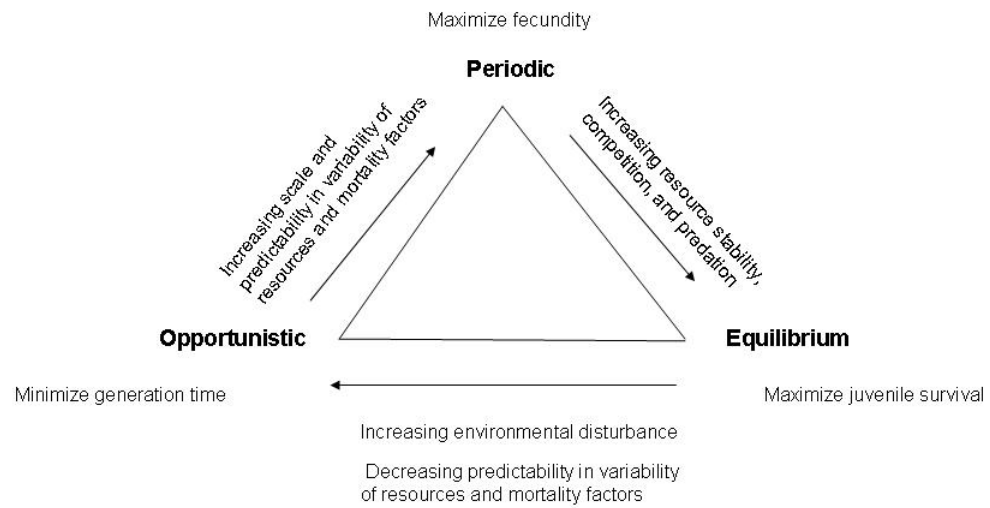**Figure 4. 1. Triangular life-history model for fishes, showing environmental gradients that select for each endpoint.** (from Winemiller and Rose, 1992)
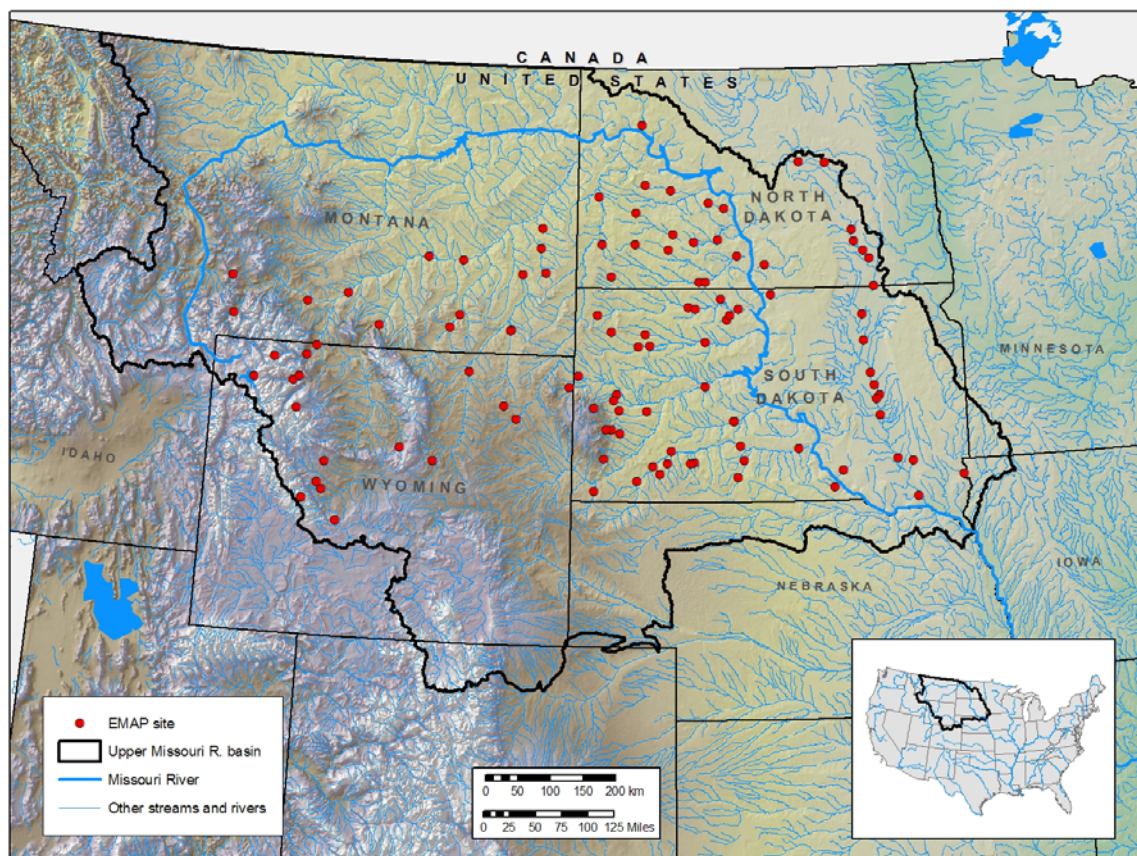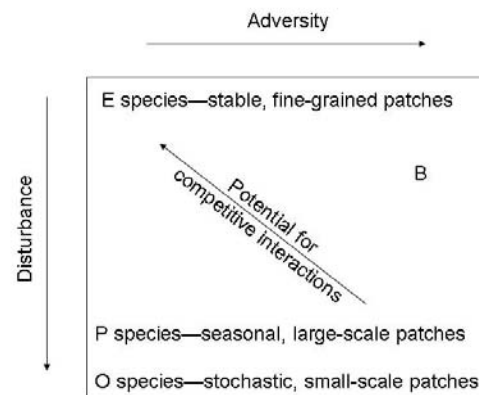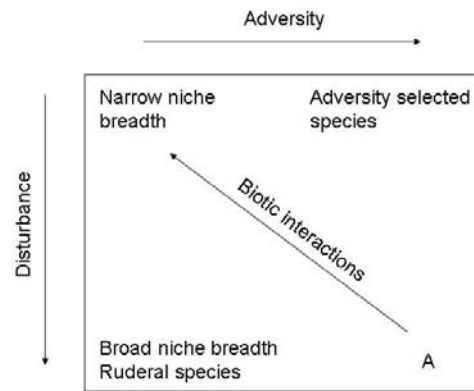
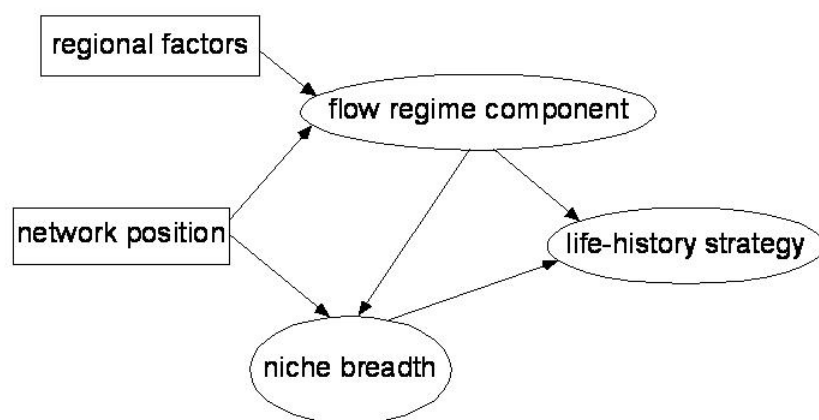**Figure 4. 2. Map of study area.**

Figure 4. 3. Habitat template theory. (A) classic predictions (Southwood, 1988) (B) specific predictions for fish life-history strategies (based on Winemiller, 2005).

Figure 4. 4. Basic conceptual model showing the interaction of factors across levels of spatial scale that shape life-history strategies.

Figure 4. 5. General SEMs for specific components of streamflow regime.
Model A, peak-flow variability; Model B, low-flow volume.
Refer to Table 4.1 for definitions of variables.
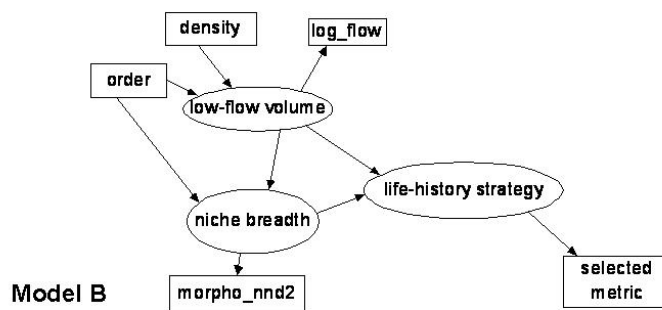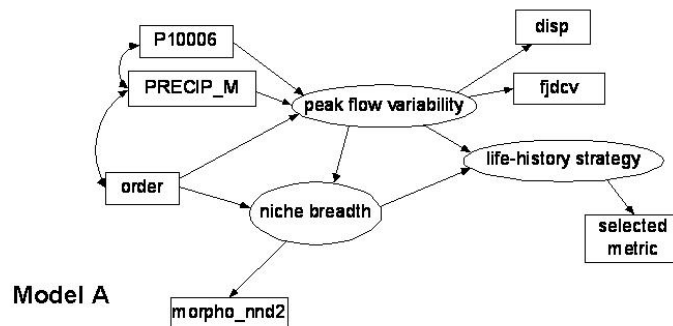
Model A

Model B

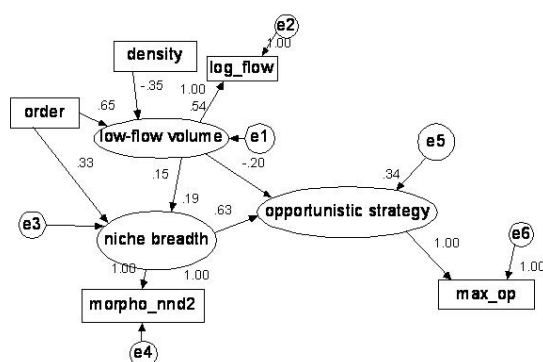**Figure 4. 6. Principal component ordination of life-history traits.**
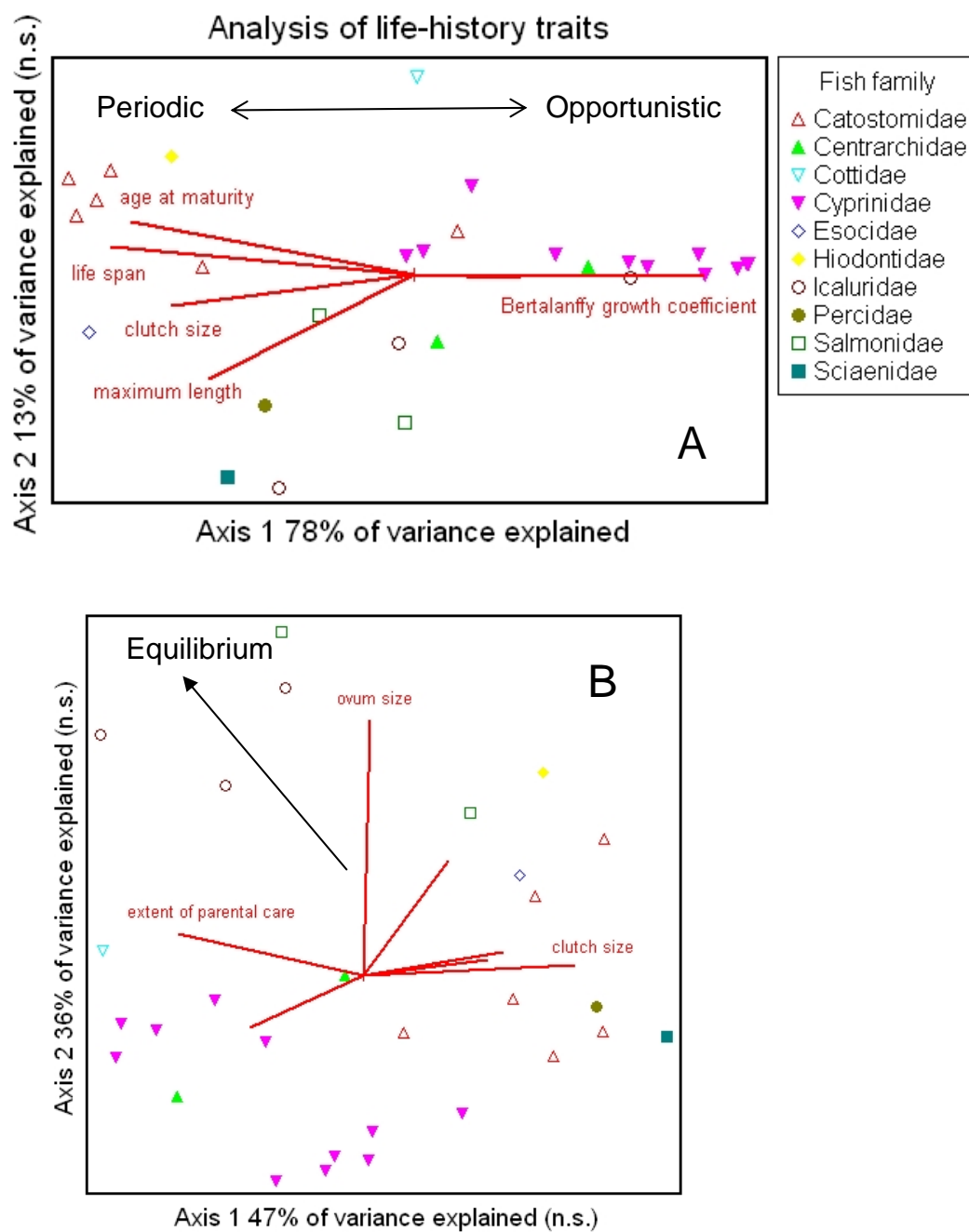
Figure 4. 7. Models relating streamflow components to the opportunistic life-history strategy.
Model A1 based on peak-flow variability; Model B1 based on low-flow volume.
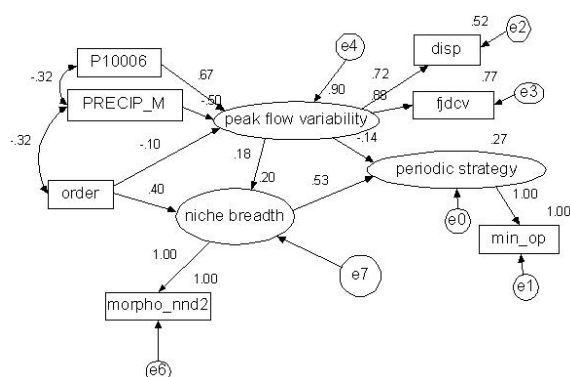Refer to Table 4.1 for definition of variables.

Standardized estimates for all sites
Chi-square = 10.890 10 df p=.366
RMSEA=.029
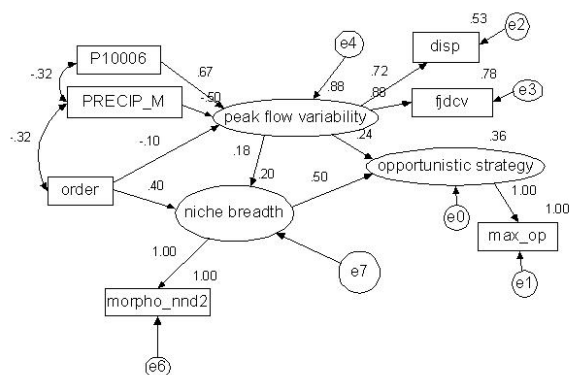
Model A1
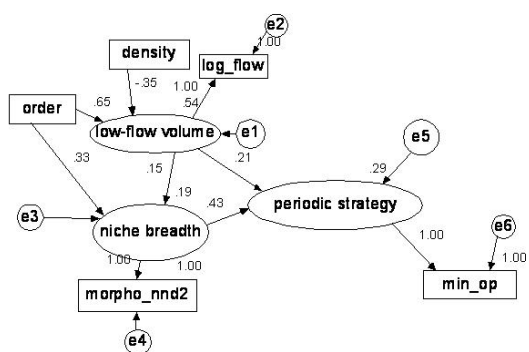

Standardized estimates for all sites
Chi-square = 6.787 (4 df) p=.148
RMSEA=.080

Model B1

Figure 4. 8. Models relating streamflow components to the periodic life-history strategy.
Model A2 based on peak-flow variability; Model B2 based on low-flow volume.
Refer to Table 4.1 for definition of variables.

Standardized estimates for all sites
Chi-square = 13.173 10 df p=.214
RMSEA=.054

Model A2

Standardized estimates for all sites
Chi-square = 4.631 (4 df) p=.327
RMSEA=.038

Model B2

Figure 4. 9. Models relating streamflow components to equilibrium strategy.
Model A3 based on peak-flow variability; Model B3 based on low-flow volume.
Refer to Table 4.1 for definition of variables.
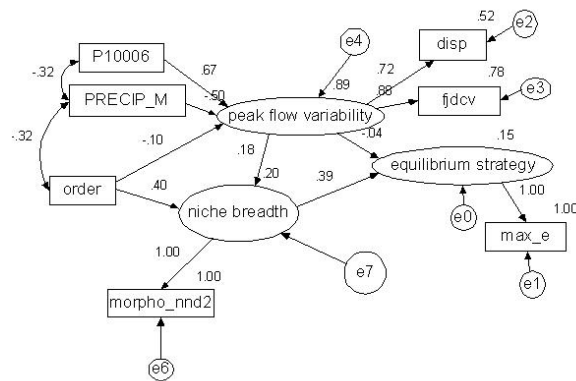
Standardized estimates for all sites
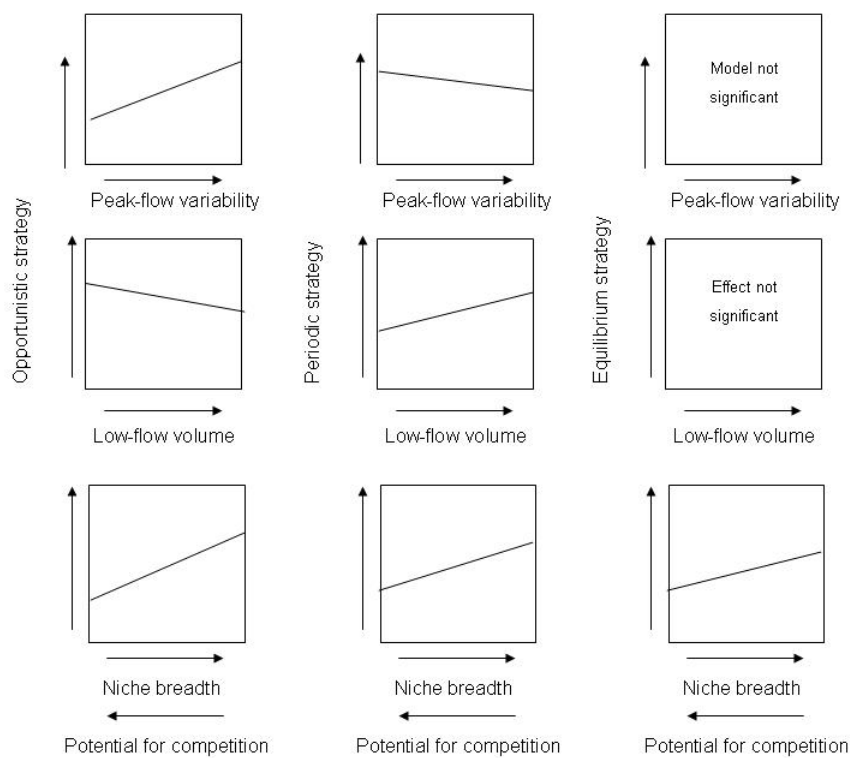Chi-square = 25.807 10 df p=.004
RMSEA=.121

Model A3
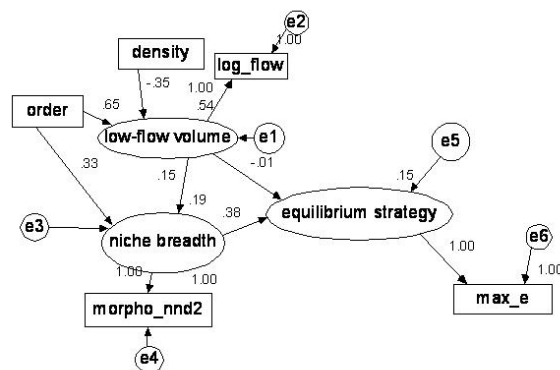
Standardized estimates for all sites
Chi-square = 8.000 (4 df) p=.092
RMSEA=.096
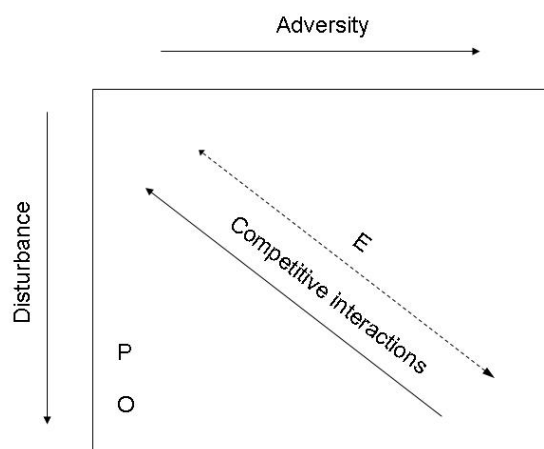
Model B3

Figure 4. 10. Overview of relations between flow and biotic factors and fish life-history strategies.

Figure 4. 11. Revised habitat template.

O species—stochastic, large-scale patches in response to regional factors
P species—stochastic, network-scale patches in response to competitive interactions
E species—wide-spread, apparently both stability and adversity selection

General Conclusions

An ecological debate is ongoing about the possibility of discovering a set of general rules that describe the organization of natural communities. On the one hand, some maintain that communities are too complex and contingent upon history and local conditions for general rules to apply without exception (Lawton, 1999; Simberloff, 2004). On the other hand, others maintain that general and predictable understanding of community organization is possible by focusing on species traits, especially their distribution in response to environmental gradients (McGill and others, 2006). This debate provides the impetus for the analyses presented in this dissertation.

My study included several approaches for using trait-based analysis to determine first, if fish assemblages were structured non-randomly, and second, what ecological processes might be associated with assemblage patterns. Fish assemblages and the factors influencing them were examined across a range of spatial scale. The largest scale was defined by large-scale hydrologic basins that were defined as integral watershed (Chapter 3), and, roughly equivalently, by regional streamflow patterns that differed significantly among them (Chapter 2). The smallest scale was represented by the sample reach, i.e. discrete assemblages, while an intermediate or meso-scale was defined by location within the stream network or stream order. This chapter provides an overview and synthesis of the results of this study, and examines their implications within the larger context of ecological monitoring and theory.

First, results clearly indicate that species co-occurrence in sample reaches is not random, but rather is structured at least in part by processes related in different ways to how similar species are to one another. The strongest effect at this level of scale appears to be from competition for trophic resources, as suggested by phylogenetic and especially phenotypic overdispersion of traits related to trophic level (Chapter 3). Some evidence was also provided for the possible impact of competition for spawning sites among species dependent on specific locations for spawning that may be limited in supply. These competitive processes may have been responsible for the the exclusion of similar species within the reach. Opposing the apparent effect of competitive exclusion was a slight tendency toward phenotypic clustering of traits

related to habitat preference, showing the effect of environmental filtering at the local scale, although this tendency was not highly significant (Chapter 3).

Second, co-occurrence within large-scale hydrologic basins was also observed to be non-random although structured by a different set of ecological traits, those related to life-history strategy. Significant large-scale phenotypic clustering, or co-occurrence of similar species, was observed for individual life-history traits including growth rate, life span, and age at maturity (Chapter 3). Similarly, significant constraints on the expression of life-history strategies within fish assemblages by large-scale regional climate patterns were also observed, as measured by multivariate measures of the same traits (Chapter 4). These climate patterns were coincident with differences in patterns of peak-flow regime across the large-scale hydrologic basins defined in this analysis (Chapter 2). Streams draining the western mountains in the Yellowstone Basin exhibited a strong snowmelt signature, with little variability in magnitude or timing of peak flow from year to year. In contrast, lowland streams in the White-Little Missouri and James-Big Sioux Basins further east showed much higher variability in peak-flow regime. These results suggest that environmental filtering of life-history traits is mediated to some extent by large-scale variability in peak-flow regime across the range of streams examined in this study.

In fishes, life-history traits are understood to be linked to form life-history strategies or syndromes of traits that represent characteristic trade-offs among three primary demographic parameters. The endpoints of these strategies are defined by traits that maximize each of these parameters in turn: opportunistic strategies maximize early onset of reproduction, periodic strategies maximize fecundity, and equilibrium strategies maximize juvenile survival (Winemiller and Rose, 1992). Evaluation of the association of these life-history strategies with large-scale influences shows a range of relationships, with only opportunistic species showing a strong response to peak-flow regime. The constraint of opportunistic species by regional factors related to peak-flow variability (Chapter 4) is consistent with the observed phenotypic clustering of life-history traits by large-scale hydrologic basin (Chapter 3). Highly opportunistic fishes are apparently constrained by low levels of peak-flow variability sufficiently enough that they are excluded from high-elevation snowmelt

streams where peak flow is not highly variable (Figure 1). The most opportunistic species found in high elevation streams, *Rhinichthys cataractae, Semotilus atromaculatus,* and *Catostomus platyrhynchus*, are relatively larger and more long-lived than the classic opportunist species observed in lowland streams. These species live longer than 10 years and achieve a maximum length of about 14 to 18 cm, compared to more opportunistic species that generally live no more than 5 years and grow to less than 10 cm (Table 4.2). In other words, the most opportunistic species in mountain stream assemblages have evolved life-history strategies that show a simultaneous tendency toward the periodic strategy, presumably because it is more adaptive under highly seasonal snowmelt conditions. These results imply that high levels of peak-flow variability may define an "envelope" of conditions for opportunistic species that is analogous to that described by nutrient dynamics for phytoplankton biomass (Harris, 1999). In other words, the available ecological space within which fish life-history strategies are distributed is apparently defined at least partially by streamflow dynamics (e.g. peak-flow variability). Accordingly, regional patterns of flow variability appear to establish a limit for the expression of the opportunistic strategy analogous to the limit defined by nutrient loads for phytoplankton biomass.

The same is evidently not true for the other life-history strategies, even though periodic fishes also reflected a significant response to peak-flow regime. In contrast to opportunistic strategists, periodic species tended to be associated with reduced peak-flow variability although the effect was less strong (Chapter 4). In fact, when the total effect of peak-flow regime and competitive potential was evaluated, the impact of flow on the distribution of these species was essentially nil. A much stronger response for these fishes was observed for factors at the network scale, including a strong preference for relatively high low-flow volume and larger-order streams. These results imply that the periodic strategy provides a certain level of resistance to the selective pressure exerted by highly variable peak flow at the annual scale, presumably because it is associated with relatively long life span and mass spawning migration. As a result, periodic strategists are apparently not vulnerable to the same regional streamflow constraints as opportunistic species.

Streamflow factors related to the distribution of equilibrium species were not resolved by this analysis. This could be because this life-history strategy is selected by its very nature to be less responsive in a consistent way to abiotic forcing functions. The focus on maximizing juvenile survival is predicted to be most adaptive in two quite different environments: relatively stable and benign conditions with high levels of biotic interactions, or relatively stressful conditions with lower levels of biotic interactions. Thus, the equilibrium strategy is quite flexible with regard to the environments in which it could be successful, which is reflected in the highly diverse group of species that demonstrated it most strongly in this study. The strongest response of equilibrium fishes to the factors evaluated in this study was a negative association with the potential for competitive interactions at the local or reach scale, which was similar to the pattern observed for the other life-history strategies.

In fact, results clearly demonstrate that fish assemblages examined in this study were structured to maximize niche breadth, or limit similarity, among component species at the local reach scale, especially with regard to trophic level. All life-history strategies were associated with this pattern. Assuming that limiting similarity is associated with competitive exclusion (Abrams, 1983), or at least strong spatial or temporal segregation between similar species, these results suggest that competition is a powerful force determining local assemblage structure. Nonetheless, it is not possible with these data to determine to what degree local assemblages reflect current competitive pressure versus the legacy of past competition. Another important limitation of the data relates to the ability to determine the effect of predation on local assemblage structure, which has been observed to be important in other studies (Hoeinghaus and others, 2007). Predation is often associated with segregation of predator and prey at the scale of micro-habitat (Power and others, 1985; Schlosser, 1987), which was impossible to evaluate with the available data.

Larger implications and limitations of the dataset utilized in this analysis are also important to consider. My study represents an attempt to utilize data collected by a large-scale monitoring program (Hughes and others, 2000) to evaluate the predictions of ecological theory and life-history models in order to identify significant factors that determine fish distribution patterns. These data were essentially collected

as "general purpose" data, however, oriented primarily toward assessment (i.e. description of current conditions) and not according to a design driven by a research agenda. As such, the use of these data to address my questions resulted in situations where additional data that would be useful were simply not available. For example, evaluating the effect of network position would have benefited from a hierarchical stratified sampling design, where similarly defined upstream and downstream stream reaches were sampled across a number of basins. In the same way, analysis of the effect of competitive potential would have been improved by size distribution data for observed fish species as well as separate samples by habitat units within each reach. On the other hand, an important strength of this approach was that comparable and consistent methods were used to collect data over a vast spatial scale, within a study area that encompasses more than 350,000 square miles (900,000 square kilometers). As such, notwithstanding the shortcomings, this dataset provided a nearly unprecedented opportunity to address questions about factors that determine fish distributions across a wide range of spatial scale.

The evaluation of predictions derived from ecological theory and conceptual models relied on structural equation modeling (SEM) because it is an approach uniquely suited to evaluating complexity. Any model of complex phenomena such as fish distribution patterns necessarily represents a simplification of the range of spatial and temporal dynamics that are involved. It is a great challenge to adequately represent significant components of complex systems in a way that advances our understanding, as well as our ability to predict the consequences of changes to these components. Results from SEM analysis indicate that stream fish assemblages are comprised of species that are differentially influenced by a hierarchy of factors ranging from large-scale abiotic constraints to local biotic interactions. Additionally, they confirm that placement of species in functional groups provides a useful perspective for successful understanding of complex patterns of fish distribution. So what are the generalizations that that can be made from these results?

My research confirms that fish distribution patterns can be significantly— though only partially—explained by the interaction of life-history traits with streamflow variability. Streamflow regime results from an integration of both large-

scale and network scale factors and acts to significantly constrain fish life histories to varying degrees. The vulnerability of each life-history strategy to flow regime is determined by the linkage or equivalence between the temporal scale of flow variability and the characteristic scale defined by the specific strategy. The extent of competitive interactions within local assemblages is an additional factor that interacts with flow regime, although my analysis does not resolve the relationship of competition with life history strategy. Nonetheless, it is clear that basic functional characteristics of fish species are described by life-history traits, including age at maturity and life span, clutch size, and ovum size. Because these ecological traits are highly evolutionarily conserved (Chapter 3), they represent critical characteristics that limit fish distribution. Life-history strategies, therefore, can be considered to be important "transition functions" (Harris, 1999) that link fish to their environment by defining temporal frequencies of streamflow components that affect distribution patterns.

References

Abrams, P., 1983. The theory of limiting similarity. Annual Review of Ecology and Systematics 14: 359-376.

Harris, G, 1999. This is not the end of limnology (or of science): the world may well be a lot simpler than we think. Freshwater Biology 42: 689-706.

Hoeinghaus, D.J., K.O. Winemiller, and J.,S. Birnbaum, 2007. Local and regional determinants of stream fish assemblage structure: inferences based on taxonomic vs. functional groups. Journal of Biogeography 34: 324-338.

Hughes, R.M., S.G. Paulsen, and J.L. Stoddard, 2000. EMAP-Surface Waters: a multiassemblage, probability survey of ecological integrity in the US.A. Hydrobiologia 422/423: 429-443.

Lawton, J.H., 1999. Are there general laws in ecology? Oikos 84: 177-192.

McGill, B.J., B.J. Enquist, E. Weiher, and M. Westoby, 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21(4): 178-185.

Power, M.E., Matthews, W.J., and A.J.Stewart, 1985. Grazing mnnows, piscivorous bass and stream algae: dynamics of a strong interaction. Ecology 66: 1448-1456.

Schlosser, I.J., 1987. The role of predation in age- and size-related habitat use by stream fishes. Ecology 68: 651-659.

Simberloff, D., 2004. Community ecology: is it time to move on? American Naturalist 163: 787-799.

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

Figure 5. 1. Distribution of opportunistic life-history strategy.
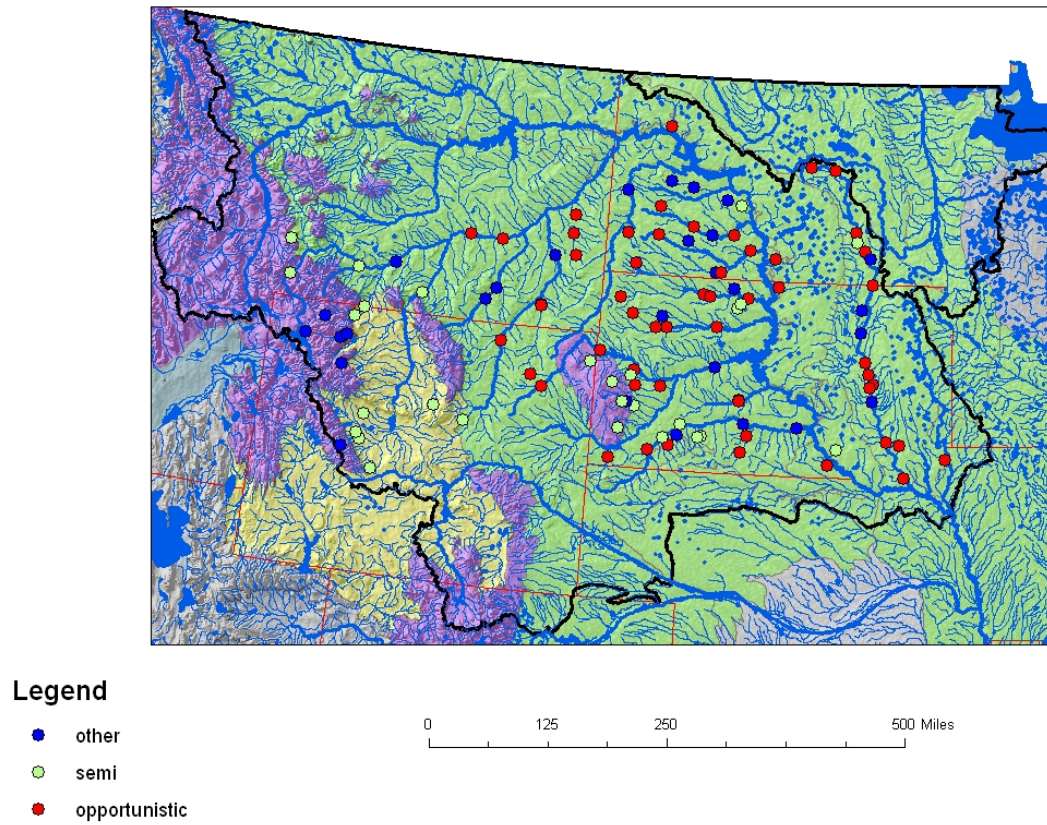
Bibliography

Balon, E.K., 1975. Reproductive guilds of fishes: a proposal and definition. Journal of the Fisheries Research Board of Canada 32: 821-864.

Biggs, B.J.F., V.I. Nikora, and T.H. Snelder, 2004. Linking scales of flow variability to lotic ecosystem structure and structure. River Research and Applications 21: 283-298.

Bunn, S.E., and A.H. Arthington, 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30(4): 492-507.

Burn, D.A., 1990a. An appraisal of the "region of influence" approach to flood frequency analysis. Hydrological Sciences 35(2): 149-165.

Burn, D.H., 1990b. Evaluation of regional flood frequency analysis with a region of influencer approach. Water Resources Research 26(10): 2257-2265.

Cavender-Bares, J,. D.D. Ackerly, D.A.Baum, and F.A.Bazzaz, 2004. Phylogenetic overdispersion in Floridian oak communities. The American Naturalist 163(6): 823-843.

Cavender-Bares, J., A. Keen, and B. Miles, 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. Ecology 87(7) Supplement: S109-S122.

Coburn, M.M. and T.M. Cavender, 1992. Interrelationships of North American cyprinid fishes, pages 329-365 *in* R.L. Mayden, (editor) Systematics, historical ecology, and North American freshwater fishes. Stanford University Press, Stanford CA.

Connell, J.H., 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35(2): 131-138.

Cunnane, C., 1988. Methods and merits of regional flood frequency analysis. Journal of Hydrology 100: 269-290.

Daly, C., R.P. Neilson, and D.L. Phillips, 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. Journal of Applied Meteorology 33: 140-158.

Davies, T.J., 2006. Evolutionary ecology: when relatives cannot live together. Current Biology 16(16): R645-R647.

Decker, L.M. and D.C. Erman, 1992. Short-term seasonal changes in composition and abundance of fish in Sagehen Creek, California. Transactions of the American Fisheries Society 121: 297-306.

Diez, J.M. and H.R. Pulliam, 2007. Hierarchical analysis of species distributions and abundance across environmental gradients. Ecology 88(12): 3144-3152.

Dodds, W.K., K. Gido, M.R. Whiles, K.M. Fritz, and W.J. Matthews, 2004. Life on the edge: the ecology of Great Plains prairie streams. BioScience 54(3): 205-216.

Fausch, K.D. and K.R. Bestgen, 1997. Ecology of fishes indigenous to the central and southwestern Great Plains. Pages 131-166 *in* Knopf and Samson (eds.) Ecology and conservation of Great Plains vertebrates. New York: Springer-Verlag.

Fausch, K.D., C.E. Torgersen, C.V. Baxter, and H.W. Li, 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52(6): 483-498.

Fausch, K.D., Y. Taniguchi, S. Nakano, G.D. Grossman, and C.R. Townsend, 2001. Flood disturbance regimes influence rainbow trout invasion success among five holarctic regions. Ecological Applications 11(5): 1438-1455.

Frissell, C.A., W.J. Liss, C.E. Warren, and M.D. Hurley, 1986. A hierarchical framework for stream habitat

Froese, R. and D. Pauly, (eds), 1998. FishBase 1998: concepts, design and data sources. ICLARM, Manila, Philippines. 293 pp.

Gatz, A.J., 1979. Community organization in fishes as indicated by morphological features. Ecology 60(4): 711-718.

- 1981. Morphologically inferred niche differentiation in stream fishes. American Midland Naturalist 106: 10-21.

Gordon, N.D., T.A. McMahon, and B.L. Finlayson, 1992. Stream hydrology, an introduction for ecologists. John Wiley & Sons. 526 pp.

Grace, J.B., 2006. Structural equation modeling and the study of natural systems. Cambridge University Press.

Grafen, A., 1989. The phylogenetic regression. Philosophical Transactions of the Royal Society of London, Series B 326: 119-157.

Greenwood, J.A., J.M. Landwehr, N. N.C. Matalas, and J.R. Wallis, 1979. Probability weighted moments: definition and relation to parameters of several distributions expressible in inverse form. Water Resources Research 15(5): 1049-1054.

Haan, C.T., 2002. Statistical methods in hydrology. Iowa State Press, Ames IA. 496 pp.

Hora, S.L., 1930. Ecology, bionomics and evolution of the torrential fauna, with species reference to the organs of attachment. Philosophical Transactions of the Royal Society 28: 171-282.

Hosking, J.R.M. and J.R. Wallis, 1993. Some statistics useful in regional frequency analysis. Water Resources Research 29(2): 271-281.

Hosking, J.R.M., J.R. Wallis, and E.F. Wood, 1985. An appraisal of the regional flood frequency procedure in the UK. Hydrological Sciences 30: 85-109.

Hughes, R.M., S.G. Paulsen, and J.L. Stoddard, 2000. EMAP-Surface Waters: a multiassemblage, probability survey of ecological integrity in the U.S.A. Hydrobiologia 422/423: 429-443.

Hutchinson, G.E., 1957. Concluding remarks. Cold Spring Harbor Symposium in quantitative biology. Volume 22: 415-427.

Kelly, V.J. and S.M. Jett, 2006. Ecologically relevant quantification of streamflow regimes in western streams. EPA/620/R-06/056, U.S. Environmental Protection Agency, Washington DC.

Konrad, C.P., A.M.D. Brasher, and J.T. May, 2008. Assessing streamflow characteristics as limiting factors on benthic invertebrate assemblages in streams across the western Unites States. Freshwater Biology 53: 1983-1998.

Landwehr, J.M., and N.C. Matalas, 1979. Probability weighted moments compared with some traditional techniques in estimating Gumbel parameters and quantiles. Water Resources Rsearch 15(5): 1055-1064.

Leibold, M., 1998. Similarity and local coexistence of species in regional biotas. Evolutionary Ecology 12: 95-100.

Leopold, L.B., 1994. A view of the river. Harvard University Press, Cambridge MA.

Lettenmaier, D.P., J.R. Wallis, and E.F. Wood, 1987. Effect of regional heterogeneity on flood frequency estimation. Water Resources Research 23: 313-324.

Levin, S.A., 1992. The problem of pattern and scale in ecology. Ecology 73: 1943-1967.

Losos, J.B. and R.E. Glor, 2003. Phylogenetic comparative methods and the geography of speciation. Trends in Ecology and Evolution 18(5): 220-227.

Lovette, I.J. and W.M. Hochachka, 2006. Simultaneous effects of phylogenetic niche conservatism and competition on avian community structure. Ecology 87(7) Supplement: S14-S28.

Lundberg, J.G., 1992. The phylogeny of ictalurid catfishes: a synthesis of recent work, pages 392-411 *in* R.L. Mayden, (editor) Systematics, historical ecology, and North American freshwater fishes. Stanford University Press, Stanford CA.

MacArthur, R. and R. Levins, 1967. The limiting similarity, convergence and divergence of coexisting species. The American Naturalist 101: 377-385.

MacArthur, R.H., 1975. The theory of the niche. Pages 159-176 *in* Population Biology and Evolution (Lewontin, R., ed). Syracuse University Press.

Matthews, W.J., R.C. Cashner, and F.P. Gelwick, 1988. Stability and persistence of fish faunas and assemblages in three Midwestern streams. Copeia 1988: 947-957.

McCune, B, and J.B.Grace, 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR.

McCune, B. and M.J. Mefford, 1999. PC_ORD. Multivariate analysis of ecological data, version 4. MjM Software Design, Gleneden Beach, Oregon, USA.

McGill, B.J., B.J. Enquist, E. Weiher, and M.Westoby, 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21: 178-185.

Meffe, G.K. and W.L. Minckley, 1987. Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran Desert stream. American Midland Naturalist 117: 177-191.

Naesje, T., B. Jonsson, J. Skurdal, 1995. Spring flood: a primary cue for hatching of river spawning Coregoninae. Canadian Journal of Fisheries and Aquatic Sciences 52: 2190-2196.

Nelson, J.S., 2006. Fishes of the world. John Wiley, Hoboken NJ.

Nesler, T.P., R. Muth, A.F. Wasowicz, 1988. Evidence for baseline flow spikes as spawning cues for Colorado squawfish in the Yampa River, Colorado. American Fisheries Society Symposium 5: 68-79.

NOAA (National Oceanographic and Atmospheric Administration), 1973. Atlas 2, Precipitation frequency atlas of the western United States. Data available on line (http://hdsc.nws.naoo.gov/hdsc/pfds/index.html).

Olden, J.D., N.L. Poff, K.R. Bestgen, 2006. Life-history strategies predict fish invasions and extirpations in the Colorado River basin. Ecological Monographs 76(1): 25-40.

Omernik, J.M., 1987. Ecoregions of the conterminous United States (map supplement): Annals of the Association of American Geographers 77(1): 118-125.

Ouarda, T.B.M.J., C. Girard, G.S. Cavadias, and B. Bobee, 2001. Regional flood frequency estimation with canonical correlation analysis. Journal of Hydrology 254: 157-173.

Palmer, M.A. and N.L. Poff, 1997. Heterogeneity in streams. Journal of the North American Benthological Society 16: 169-173.

Partridge, L. and P.H. Harvey, 1988. The ecological context of life history evolution. Science 241(4872): 1499-1455.

Peck, D.V., Herlihy, A.T., Hill, B.H., Hughes, R.M., Kaufmann, P.R., Klemm, D.J., Lazorchak, J.M., McCormick, F.H., Peterson, S.A., Ringold, P.L., Magee, T., Cappaert, M., 2006. Environmental Monitoring and Assessment Program-Surface Waters Western Pilot Study: Field Operations Manual for Wadeable Streams. EPA/620/R-06/003, U.S. Environmental Protection Agency, Office of Research and Development, Washington, DC.

Peckarsky, B.L., 1983. Biotic interactions or abiotic limitations? A model of lotic community structure. Pages 303-323 *in* Dynamics of lotic ecosystems (T.D. Fontaine and S.M. Bartell, eds). Ann Arbor Science, Ann Arbor, MI.

Poff, N.L. and J.V. Ward, 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Canadian Journal of Fisheries and Aquatic Sciences 46: 1805-1818.

Poff, N.L., 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of North American Benthological Society 16: 391-409.

Poff, N.L., and J.D. Allan, 1995. Functional organization of stream fish assemblages in relation to hydrological variability. Ecology 76(2): 606-627.

Poff, N.L., J.D. Allan, M.B. Bain, J.R. Karr, K.L. Prestegaard, B.C.Richter, R.E. Sparks, and J.C. Stromberg, 1997. The natural flow regime. Bioscience 47(11): 769-784.

Poff, N.L., J.D. Olden, N.K.M. Vieira, D.S. Finn, M.P. Simmons, and B.C. Kondratieff, 2006. Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. Journal of North American Benthological Society 25(4): 730-755.

Puckridge, J.T., F. Sheldon, K.F. Walker, and .A.J. Boulton, 1998. Flow variability and the ecology of large rivers. Marine and Freshwater Research 49: 55-72.

Rahel, F.J., 1990. The hierarchical nature of community persistence: a problem of scale. The American Naturalist 136: 328-344.

Raley, M.E. and R.M. Wood, 2001. Molecular systematics of members of the *Notropis dorsalis* species group (Actinopterygii: Cyprinidae). Copeia 200(3): 638-645.

Reice, S.E., R.C. Wissmar, and R.J. Naiman, 1990. Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. Environmental Management 14(5): 647-659.

Resh, V.H., A.V. Brown, A.P. Covich, M.E. Gurtz, H.W. Li, G.W. Minshall, S.R. Reice, A.L. Sheldon, J.B. Wallace, and R.C. Wissmar, 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7(4): 433-455.

Ricklefs, R.E. and D. Schluter, 1993. Species fiversity in ecological communities. University of Chicago Press, Chicago, Illinois.

SAS Institute, Inc., 1989. SAS/STAT users guide, version 6, 4th edition, volume 1 and 2, Cary NC. 1,686 pp.

Scheidegger, K.J. and M.B. Bain, 1995. Larval fish distribution and microhabitat use in natural and regulated rivers. Copeia 1995: 125-135.

Schlosser, I.J., 1991. Stream fish ecology: a landscape perspective. BioScience 41: 704-712.

Schoener, T.W., 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51: 408-418.

Schwartz, G.E. and Alexander, R.B., 1995. State soil geographic (STATSGO) data base for the conterminous United States. U.S. Geological Survey, Open-File Report 95-449.

Seaber, P.R., F.P. Kapinos, and G.L. Knapp, 1987. Hydrologic unit maps. U.S. Geological Survey Water-Supply Paper 2294.

Seegrist, D.W. and Gard, R., 1972. Effects of floods on trout in Sagehen Creek, California. Transactions of the American Fisheries Society 101: 478-482.

Simmers, I., 1975. The use of regional hydrology concepts for spatial translation of streamflow data. International Association of Hydrologic Sciences Publication 117: 109-117.

Smakhtin, V.U., 2001. Low flow hydrology: a review. Journal of Hydrology 240: 147-186.

Smith, G.R., 1992. Phylogeny and biogeography of the Catostomidae, freshwater fishes of North America and Asia, pages 778-827 *in* R.L. Mayden, (editor) Systematics, historical ecology, and North American freshwater fishes. Stanford University Press, Stanford CA.

Southwood, T.R.E., 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology 46: 337-365.

- 1988. Tactics, strategies and templets. Oikos 52: 3-18.

Statzner, B., J.A. Gore, and V.H. Resh, 1988. Hydraulic stream ecology: observed patterns and potential applications. Journal of North American Benthological Society 7: 307-360.

Stearns, S.C., 1976. Life-history tactics: a review of the ideas. The Quarterly Review of Biology 51(1): 3-47.

Stedinger, J.R., R.M.Vogel, and E.Foufoula-Geoergiou, 1993. Frequency analysis of extreme events, p. 18.1-18.66 *in* D.R. Maidment (ed.) Handbook of hydrology. McGraw-Hill, Inc.

Stevens, D.L. Jr., and A.R. Olsen, 1999. Spatially restricted surveys over time for aquatic resources. Journal of agricultural, Biological, and Environmental Statistics 4(4): 415-428.

Stoddard, J.L., D.V. Peck, S.G. Paulsen, J. Van Sickle, C.P. Hawkins, A.T. Herlihy, R.M. Hughes, P.R. Kaufmann, D.P. Larsen, G. Lomnicky, A.R. Olsen, S.A. Peterson, P.L. Ringold, and T.R. Whittier, 2005. An ecological assessment of western streams and rivers. EPA 620/R-05/005, U.S. Environmental Protection Agency, Washington DC.

Tabachnich, B.G. and L.S. Fidell, 2000. Using multivariate statistics, 4th edition. Allyn and Bacon, Needham Heights, MA.

Tilman, D., 1976. Ecological competition between algae: experimental confirmation of resource-based competition theory. Science 192: 463-465.

Townsend, C.R., and A.G. Hildrew, 1994. Species traits in relation to a habitat templet for river systems. Freshwater Biology 31: 265-275.

USDC (U.S. Department of Commerce), 1961. East U.S. rainfall frequency, Technical Paper No. 40, U.S. Department of Commerce, Weather Bureau.

USEPA, 2006. Level III ecoregions of the conterminous United States. URL http://www.epa.gov/wed/pages/ecoregions/level_iii.htm, accessed March 2006).

Vogelmann, J.E., T.L. Sohl, P.V. Campbell, and D.M. Shaw, 1998. Regional land cover characterization using Landsat Thematic mapper data and ancillary data sources. Environmental Monitoring and Assessment 51(1-2): 415-428.

Ward, J.V., and J.A. Stanford, 1983. The intermediate disturbance hypothesis: an explanation for biotic diversity patterns in lotic ecosystems, p. 327-356 *in* E.D. Fontaine, III and S.M. Bartell (eds.) Dynamics of lotic ecosystems. Ann Arbor Press, Ann Arbor MI.

Webb, C.O., D.D. Ackerly, M.A. McPeek, and M.J. Donoghue, 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics 33: 475-505.

Weldon, C.W. and W.L. Slauson, 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. The Quarterly Review of Biology 61(1): 23-44.

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

Wiens, J.J. and C.H. Graham 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology and Systematics 36: 519-539.

Williams, D.D. and H.B.N. Hynes, 1977. The ecology of temporary streams. II. General remarks on temporary streams. Internationale Revue des gesampten Hydrobiologie 62: 53-61.

Wiltshire, S.E., 1986. Identification of homogeneous regions for flood frequency analysis. Journal of Hydrology 84: 287-302.

Winemiller, K.O., 1991. Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. Ecological Monographs 61(4): 343-365.

- 2005. Life history strategies, population regulation, and implications for fisheries management. Canadian Journal of Fisheries and Aquatic Sciences 62: 872-885.

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

Winston, M.R., 1995. Co-occurrence of morphologically similar species of stream fishes. The American Naturalist 145(4): 527-545.

Zrinji, Z. and D.H. Burn, 1994. Flood frequency analysis for ungaged sites using a region of influence approach. Journal of Hydrology 153: 1-21.