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FUNCTIONAL ORGANIZATION OF STREAM FISH ASSEMBLAGES IN RELATION TO HYDROLOGICAL VARIABILITY[1]

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Abstract. Stream fish assemblage data for 34 sites in Wisconsin and Minnesota were obtained from archived sources and were used in conjunction with long-term hydrological data to test the hypothesis that functional organization of fish communities is related to hydrological variability. For each of the 106 species present in the data set, six categories of species traits were derived to describe habitat, trophic, morphological, and tolerance characteristics. A hierarchical clustering routine was used to identify two functionally similar groups of assemblages defined in terms of species presence/absence. Hydrological factors describing streamflow variability and predictability, as well as frequency and predictability of high flow and low flow extremes, were derived for each of the 34 sites and employed to explain differences among the functionally defined groups. Canonical discriminant analysis revealed that the hydrological data could clearly separate the two ecologically defined groups of assemblages, which were associated with either hydrologically variable streams (high coefficient of variation of daily flows, moderate frequency of spates) or hydrologically stable streams (high predictability of daily flows, stable baseflow conditions). Discriminant functions based on hydrological information classified the 34 fish assemblages into the correct ecological group with 85% accuracy. Assemblages from hydrologically variable sites had generalized feeding strategies, were associated with silt and general substrata, were characterized by slow-velocity species with headwater affinities, and were tolerant to silt. Proportions of species traits present at the 34 sites were regressed against an index of hydrological stability derived from a principal components analysis to test the hypothesis that functional organization of assemblages varied across a gradient of hydrological stability. Results were complementary with the discriminant analysis. Findings were in general agreement with theoretical predictions that variable habitats should support resource generalists while stable habitats should be characterized by a higher proportion of specialist species. Several species of fish were identified as indicative of the variable–stable hydrological gradient among stream sites. A taxonomic analysis showed strong geographic patterns in species composition of the 34 assemblages. However, zoogeographic constraints did not explain the observed relationship between stream hydrology and functional organization of fish assemblages. The strong hydrological–assemblage relations found in the 34 midwestern sites suggest that hydrological factors are significant environmental variables influencing fish assemblage structure, and that hydrological alterations induced by climate change (or other anthropogenic disturbances) could modify stream fish assemblage structure in this region.

Key words: community assembly; community structure; environmental variability; fishes; hydrological regime; midwestern U.S.; physical habitat template; regional patterns; scale; species traits; streams.

INTRODUCTION

An emerging view in community ecology is that local assemblage organization is constrained not only by local processes, but also by larger scale environmental factors and available species pool (Ricklefs 1987, Roughgarden 1989, Menge and Olson 1990, Ricklefs and Schluter 1993). This implies that when ecological generalizations are sought at regional scales, information on abiotic constraining factors and historical processes (including biogeography) must be explicitly included to understand any observed patterns, though local processes or habitat constraints may also need to be invoked to explain residual variation in the regional pattern (Duarte 1991).

Hydrological regime is a significant constraint on lotic assemblage structure. Extremes of flow and patterns of flow variability can directly influence local community structure, as has been demonstrated by a number of studies for both fish (Horwitz 1978, Meffe 1984, Coon 1987, Bain et al. 1988, Jowett and Duncan 1990, Fausch and Bramblett 1991) and invertebrates

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(reviewed in Poff and Ward 1989, Fisher and Grimm 1991). For individual fish species, spates cause direct mortality for both juveniles (e.g., Seegrist and Gard 1972, Schlosser 1985, Harvey 1987) and adults (e.g., Harrell 1978, Toth et al. 1982), and the timing of high flows may serve as an environmental cue for spawning (John 1963, Nesler et al. 1988). As the importance of physical disturbance to streams becomes increasingly recognized (Resh et al. 1988), interest has grown in testing the hypothesis that significant variation in assemblage structure among streams is explicable in terms of hydrological patterns, which can vary substantially over even short geographic distances (Poff and Ward 1989, Biggs et al. 1990, Poff and Allan 1993).

In attempting to identify environmental determinants of assemblage structure across geographic domains, assemblages and environmental factors should be viewed at comparable scales (see O'Neill et al. 1986, Wiens 1989, Levin 1992). Margalef (1968) pointed out that large-scale patterns are best detected with coarse-grain data. For ecological communities relative abundance data provide fine-grain information because they emphasize local peaks in species performance, while species presence/absence data emphasize a coarser grain of environmental tolerance (Allen and Starr 1982, cf. Rahel 1990). In streams, availability of long-term discharge data allows great flexibility in describing environmental variability in ecologically relevant terms (Poff and Ward 1989). Both fine-grained and coarse-grained hydrological descriptors can be derived, depending on the temporal resolution with which the data are viewed.

Perceived patterns of community structure are also influenced by the method of aggregation of ecological entities. Assemblages can be viewed in either taxonomic terms (species identities) or in functional terms (e.g, aggregations of species into guilds). When investigating environment–community patterns at large spatial scales, across which species compositions naturally change due to biogeographic constraints, a functional perspective allows comparison of taxonomically dissimilar assemblages (see Schoener 1986, Keddy 1994). Such functional analyses are the basis for much of comparative community ecology of both stream fish (Karr et al. 1986) and invertebrates (Vannote et al. 1980). This functional approach underscores the theoretical expectation that species traits that promote local persistence will change along environmental gradients (Connell and Orias 1964, Southwood 1977, 1988), thus perhaps giving rise to predictable rules of community assembly (see Keddy 1992). At the extremes, constant environments should be typified by strongly interactive specialist species limited by stable resources, while fluctuating environments should contain weakly interactive opportunists with generalized strategies for exploiting frequently changing resources. The ecological characteristics predicted from physical habitat constraints (the "habitat templet" of Southwood 1977, 1988) have been proposed as a particularly useful theoretical construct for assessing organization of stream communities (Schlosser 1987, 1990, Minshall 1988, Poff and Ward 1990, Poff 1992*a,* Townsend and Hildrew 1994).

To the extent that assemblage structure can be related to hydrological regime, insight may be gained into how hydrological modifications may affect stream fish assemblages. This approach has particular value for regional-scale phenomena, such as climate change, which may modify hydrological regimes across broad areas (see Poff 1992*b*). In this context, there is growing recognition of the need for large-scale comparative studies to address questions of general patterns that cannot be feasibly examined with small-scale mechanistic experiments (e.g., Pace 1991). Comparative studies can be used to test large-scale hypotheses (Diamond 1986, Ricklefs 1987, Brown and Maurer 1989), assuming sites for comparison are well matched and historical processes are comparable across sites (Tonn et al. 1990). The comparative approach has been successfully applied previously to understanding structure of fish assemblages at geographic scales (Horwitz 1978, Mahon 1984, Jackson and Harvey 1989, Tonn et al. 1990).

The first objective of this study was to test the hypothesis that variation in fish assemblage structure in lotic ecosystems is explained by hydrological variability, as proposed by Poff and Ward (1989). Numerous studies have shown that the ecology and distribution of individual fish species are strongly influenced by habitat volume (water depth), current velocity, food availability, and thermal regime, all of which are under hydrological influence. Therefore, we characterized species in functional terms sensitive to these critical environmental factors by extracting information from the published literature and from expert opinion. We also indexed environmental variability and habitat stability from long-term hydrological records. Using fish assemblage and hydrological data from 34 streams in Wisconsin and Minnesota, we defined assemblages in terms of functional similarity and tested the hypothesis that specific hydrological factors could account for among-stream variation in fish assemblage structure. A second objective was to determine whether any association between hydrological regime and fish assemblage structure corresponded to theoretical expectations, e.g., whether species in hydrologically variable environments were mostly resource generalists. A third objective of the research was to determine whether the functional analysis revealed patterns that were more informative than patterns discerned through a more traditional taxonomic approach where the ecological units are individual species identities.

METHODS

Hydrological data

All hydrological data were acquired from a commercially available database (EarthInfo 1990) that consists of a digital compilation of the U.S. Geological Survey (USGS) daily and peak values files on CD-ROM. All USGS-gauged stream sites in Wisconsin and Minnesota that were in proximity to an available fish sampling station were screened for unacceptable sources of hydrological disturbance (impoundment, hydroelectric facilities, irrigation withdrawal, etc.). The acceptability of the candidate sites was verified by referring to an independently derived data set that lists streams having long-term unmodified flow regimes (Slack and Landwehr 1992) and by personal communication with USGS personnel.

Eight variables were derived for each gauged site from the long-term hydrological data set to describe variability and predictability of average streamflow conditions and to describe frequency and predictability of high flow and low flow extremes. Average streamflow conditions were indexed by two variables. Coefficient of variation of daily flow is a dimensionless index that represents the ratio of the mean daily flow over the period of record to the standard deviation of the daily flows, multiplied by 100 and expressed as a percent. It describes overall flow variability without considering the temporal sequence of flow variation. Predictability of daily flow is defined by an index developed by Colwell (1974). The index ranges in value from 0 to 100% and is composed of two independent, additive components: constancy (C), a measure of temporal invariance, and contingency (M), a measure of periodicity (see Colwell 1974, Poff and Ward 1989 for more details). The index can be used to express the degree to which flow "states" (here, quantity of discharge) are predictably distributed across specified time intervals (here, days). Eleven categories were defined by a $\log_2$ series with boundaries at 2^{-3}, 2^{-2}, 2^{-1}, 2^0, 2^1, 2^2, 2^3, 2^4, 2^5, and 2^6 times mean flow. Thus, the 11 flow states ranged from <12.5% of mean flow to >640% of mean flow.

Extreme flow events were divided into high flows (spates) and low flows. Spates are defined as flows exceeding "bankfull," a level of flow that maintains channel form (Dunne and Leopold 1978) and that can be viewed as an objective measure of disturbance (Poff and Ward 1989). Bankfull discharge was determined for a stream by analyzing the annual instantaneous peak flow series and calculating the level of flow that occurs on average once every 1.67 yr based on a lognormal distribution (see Dunne and Leopold 1978). By regressing instantaneous peak flows onto the average daily flow values occurring on the same annual dates, we derived an index of bankfull discharge that could be applied to the continuous, long-term daily flow record (see Poff and Ward 1989, Poff and Allan 1993 for more details). Spate frequency is defined as the average number of spates per year. Spate predictability is a seasonal variable that indexed the proportion of all spates that fall in any 60-d "seasonal window" over the entire period of record. This variable ranges from 0.167 (uniform distribution among seasons) to 1.0 (perfectly seasonally predictable). Spate-free period is the maximum proportion of the year during which no spates have ever occurred over the period of record.

Low flows were characterized by identifying periods of below average discharge and by calculating site-specific lowflows of specified return intervals (see Poff and Ward 1989, Poff and Allan 1993). Baseflow stability is a measure of how buffered the stream is against intermittency. It is a dimensionless index derived by averaging the annual ratios of the lowest daily flow to the mean daily flow. To determine the lowflow regime for a site, the annual 1-d minimum 24-h low flow values were used, with the assumption that they represent a sample from a population with a Gumbel (extreme value) distribution (Linsley et al. 1982:375). The parameters from this distribution were used for each station to calculate the 1-d lowflow value with a 5-yr recurrence interval, a threshold arbitrarily determined to represent an important lowflow event. Lowflow predictability is the proportion of lowflow events ≥5-yr magnitude falling in a 60-d "seasonal window" (as described above for spate predictability). Lowflow-free period is the maximum proportion of the year during which no lowflow events have ever occurred over the period of record.

Fish data

Sites with pre-existing fish survey data in Wisconsin and Minnesota were taken from the Master Fish and Waterbody file from the Wisconsin Department of Natural Resources (Fago 1992), and a stream survey from the University of Minnesota Bell Museum of Natural History. Data currently are housed in the Global Climate Change Information Management Systems in the Environmental Protection Agency's (EPA) Environmental Research Laboratory in Duluth, Minnesota.

Data collected in this fashion pose problems, including variable motivations for collection, dissimilar collection techniques and sampling periods, and differential taxonomic resolution and accuracy across sites. Despite these limitations, archived (historical) fish collection data can be used to examine specific ecological hypotheses (e.g., Horwitz 1978), though the strength of the interpretations must be qualified by the uncertain quality of the available data.

For each USGS-gauged site, a map was generated that showed the local stream network and the locations of all fish sampling sites in the vicinity of the gauge. Acceptability of fish data was determined from several criteria established a priori. First, any survey sample collected within a 15 km radius of a gauge, a distance we considered representative of hydrological conditions at the gauge, was considered a candidate sample. Second, survey samples taken from small tributaries or in lentic habitats adjacent to the gauged stream were excluded. Third, only collections taken since 1960 were included to keep the data relatively contemporary.

Fourth, candidate sites with <20 species present across all combined collections were rejected. All species identified across all collections were collapsed into one fish assemblage matrix per site to diminish the likelihood that any observed patterns in assemblage structure across sites might simply reflect inadequate sampling intensity. The criterion of presence of at least 20 species created a bias against inclusion of very small streams with naturally low diversity; however, very small streams were not included in the database from the outset because most USGS gauges in this region occur on mid-sized streams or rivers. Our approach represented a trade-off between minimizing artifacts caused by sampling intensity and retaining enough sites in the database to perform a valid analysis. In Wisconsin and Minnesota, 25 and 9 sites, respectively, contained at least 20 species and were acceptable hydrologically. These 34 sites constitute a regional data set derived from assemblages sharing common drainages.

Although many sites contained abundance data for individual fish species, we considered presence/absence data to provide the proper ecological grain for testing long-term adjustment of assemblage structure to average hydrological environment. Further, because abundance data are relatively sensitive to sampling techniques and effort, we did not consider them to be reliable in making among-site or among-year comparisons. Therefore, we collapsed all data into a binary form.

Derivation of functional measures

Trophic guild.—A number of authors have proposed trophic or feeding categories for stream fishes (e.g., Allen 1971, Horwitz 1978, Moyle and Li 1979, Grossman et al. 1982, Schlosser 1982). Trophic guilds are necessarily approximate because stream fishes are known to be flexible in their diets, feed opportunistically based on food availability, and undergo ontogenetic shifts in feeding role. However, how fishes obtain their food (e.g., from the water column vs. the benthos) helps to discriminate among trophic guilds. Overlap in diet has been addressed in some studies by setting boundaries based on relative frequency of food items (e.g., Schlosser (1982) sets the boundary between omnivore and herbivore at >25% plant matter) or by assigning a species to multiple categories (e.g., Grossman et al. 1982). Such decisions may be most suitable to a study of a specific fish assemblage that includes inspection of stomach contents. Because our analysis is based on collections over broad regions and did not include direct diet analysis, we used the principal food and feeding mode of the adult. This approach also was taken by Horwitz (1978). Fishes were assigned to the trophic categories presented in Table 1. Diet and mode of feeding were determined for adult fishes based on descriptions in Becker (1983). Fishes whose diet included substantial plant matter were classified as herbivore-detritivores, while those reported to ingest only occasional amounts of plant matter were classified as omnivores. Invertivores were further defined as feeding primarily from the benthos, from the water column and surface, or in a generalized fashion.

Habitat classification.—Habitat preferences were established from references describing stream fishes from the midwestern region of North America (Scott and Crossman 1973, Lee et al. 1980, Trautman 1981, Becker 1983). Because there are no generally accepted habitat categories that parallel trophic categories, we first examined habitat descriptions from standard references, and then developed categories that appeared to allow useful separation of species into major habitat categories. Stream size association is a correlate of required water depth or habitat volume, an important factor affecting species' distributions (e.g., Gorman and Karr 1978). A fish species' current velocity preference expresses the influence that water movement has on fish species distribution. Among other factors, fish must pay an energy cost to maintain position in moving water (e.g., Fausch 1984). The third habitat variable defined for individual fish was substratum preference, which helps define a species' requirements for food, shelter, and/or reproduction. Efforts to place species into habitat categories were hampered to varying degrees either by lack of specific information in published descriptions, or by the species' apparent breadth of habitat use. Because of the latter, in a number of instances it was necessary to use a "general" category.

Tolerance to silt.—Tolerance to silt is based on expert opinion. An existing database (Ohio EPA 1989) classifed many of our species. The remaining species were given tolerance scores based on references cited above and on expert opinion. Three tolerance categories were established (Table 1).

Body morphology measurements.—Fish body morphology often varies among different lotic biotypes (Nikolskii 1963, cf. Gatz 1979). Based on limited work, it appears that dominant morphological types in lotic fish assemblages can be influenced by hydrological variability (Bain et al. 1988, Scarnecchia 1988). Two morphological ratios (Webb and Weihs 1986) that are likely to vary with hydrological environment were examined. The shape factor was defined by the ratio of total body length to maximum body depth, and it has been called the fineness ratio (Scarnecchia 1988). It describes the hydrodynamic profile of the fish (e.g., fusiform vs. bluff body profile) and influences energy costs of position maintenance. A swimming factor was defined as the ratio of minimum depth of the caudal peduncle to the maximum caudal fin depth. Fish having a small ratio are capable of strong, sustained swimming (e.g., thunniform fishes). Morphological measurements for fishes were taken from pictures and drawings mainly from Page and Burr (1991) and Lee et al. (1980), though measurements for three species were taken from Scott and Crossman (1973) and Trautman (1981).

Validation.—Many species inhabited a range of cat-

TABLE 1. Six functional measures (in 25 subcategories) for fish species. All measures are categorical variables with the exception of the morphology, which is continuous.

- Trophic guild
  1. Herbivore-detritivore
  2. Omnivore
  3. General invertivore
  4. Surface/water column invertivore
  5. Benthic invertivore
  6. Piscivore*
  7. Planktivore
  8. Parasite
- Habitat classification
  - Stream size preference
    1. Small†
    2. Medium-Large‡
    3. Small-Large§
    4. Lentic
  - Current velocity preference
    1. Fast
    2. Moderate
    3. Slow-none
    4. General
  - Substratum preference
    1. Rubble (rocky, gravel)
    2. Sand
    3. Silt
    4. General
- Tolerance
  1. High
  2. Medium
  3. Low
- Body morphology
  1. Swimming factor
  2. Shape factor

* Includes fishes feeding on crayfish.

† Fishes of small streams and headwaters, and of both small and medium streams.

‡ Found in medium-sized streams and large rivers.

§ Reported in small, medium, and large streams and rivers.

egories, and information varied in its completeness. After developing the categories of Table 1 and assigning each species a code based on available literature, results were submitted to expert fish biologists familiar with the regional ichthyofauna for evaluation (G. R. Smith, Museum of Zoology, University of Michigan and Paul R. Seelbach, Institute for Fisheries Research, Michigan Department of Natural Resources). This expert judgment supported our trophic and habitat characterizations, and provided additional information for ≈10% of the species where some information was lacking.

Data analysis

Our primary goal was to determine if variation in functional organization of fish assemblages could be explained by variation in hydrological conditions. Therefore, we adopted the two-stage approach of "community interpretation" (Ludwig and Reynolds 1988:277 ff.). The first step was to use the species functional data to classify the 34 assemblages into ecologically similar, homogeneous groups, using all species traits simultaneously. The second step was to interpret these ecological groups by testing for differences in environmental (hydrological) factors associated with each of the groups. If assemblages respond differentially to differences in environmental factors, then group membership will correlate strongly to the environmental factors. Additionally, we ordinated the 34 sites along a gradient of hydrological variability to determine whether the occurrences of individual species traits across the 34 sites were dependent on hydrological variability.

Functional structure of fish assemblages.—For each species in the overall data set, functional information was available for six individual categories (25 total subcategories, resulting in a 34 site × 25 attribute matrix). For the continuous (morphological) variables, the average value for all species present was calculated for each site. Thus, for a site with 40 species, the value entered in the matrix for the first morphology attribute was calculated by averaging together the 40 species' values for that attribute. For categorical variables, the proportion of all species falling into subcategories within a major category was determined. The trophic category, for example, contained eight subcategories. If 10 of 40 species present were omnivores, and 4 species were herbivores, then 0.25 and 0.10 would be entered as the omnivore and herbivore attribute scores, respectively, for that site. All subcategory scores summed to 1.00 (slightly less in rare cases where a species with an undefined attribute occurred) for each of the five major categorical attributes. After the matrix was constructed, a 34 × 34 similarity matrix was derived that described the correlation among sites in the functional attribute space (i.e., sites with functionally similar fish assemblages would be highly correlated). This similarity matrix was used as input into a hierarchical cluster analysis (Ward's method) using SAS (1988). All clustering methods have analytical limitations (Milligan 1980), and may be best thought of as descriptive methods for pattern analysis. A desirable feature of Ward's method is that it allows the user to specify the number of ecologically similar groups to be identified. Because we were primarily interested in determining associations between fish assemblage structure and hydrological regime, we examined the functional organization of these ecologically similar groups only after we determined their relationship to the hydrological variables.

Discrimination of fish assemblage structure by hydrological variables.—To test the null hypothesis that these functionally defined groups were not explicable in terms of independent hydrological variables, we employed discriminant analysis (SAS 1988). This parametric technique, which has been used extensively in the ecological literature (see Ludwig and Reynolds 1988, Williams and Titus 1988), including studies of fish ecology (e.g., Hawkes et al. 1986, Bozek and Hubert 1992, Nelson et al. 1992), can be used in both a descriptive and predictive mode (Williams 1983). In both cases, the analysis consists of grouped observations (here, the ecologically similar sites) and independent measurement variables (here, the hydrological factors). The descriptive canonical discriminant analysis (CDA) derives canonical variates (linear combinations of measurement variables) that have the highest possible multiple correlation with the previously defined classes to maximally separate the groups. The predictive mode (discriminant function analysis) derives functions that can be used to classify new observations. These discriminant functions can also be used to assess the classification error rate for original ecological groupings based solely on the hydrological variables. The assumption of multivariate normality was evaluated following the advice of Johnson and Wichern (1982:156) by examining the univariate and bivariate distributions of the hydrological variables used in the CDA. Normal probability plots and chi-square probability plots (for bivariate distributions) were generated with SYSTAT (Wilkinson 1989). All the hydrological variables ultimately used in the analysis were reasonably normally distributed, as were the bivariate distributions for all pairwise combinations of these variables.

Our primary interest was in deriving canonical variates that clearly separate ecologically defined groups in hydrological data space. We initially included all eight hydrological variables in a CDA, but then excluded variables with low explanatory power (i.e., those with univariate F statistics $\leqslant 2$) in order to keep our ratio of group sample sizes to quantitative variables at the recommended 3 to 1 (Williams and Titus 1988). We repeated the analysis for several a priori ecological group sizes to determine the maximum extent to which the hydrological data could explain ecological patterns. We followed this procedure with a discriminant function analysis to assess classification error rates.

Functional organization of fish assemblages under different hydrological regimes.—For the major functional attributes, a t test was used to test the hypothesis of no statistically significant difference among the two ecological groups for each of the 25 species traits. Homoscedasticity of residuals was enhanced by log transforming the two morphological variables and arcsine transforming the proportional data prior to performing t tests (Steel and Torrie 1980). Because the proportions of species traits in the various categories for a given functional variable summed to 1.0, t tests for differences among groups for related categories of proportional data are not strictly independent. For example, if one group of sites contained a significantly higher proportion of silt-tolerant species than the second group, then the second group would very likely contain a significantly greater proportion of intolerant species. Because of this lack of independence, we also plotted means and standard errors for the groups so that the results could be evaluated graphically. The unprotected P values are reported for each of the multiple t tests.

Changes in functional organization of fish assemblages along a gradient of hydrological variability among streams were also examined. The functional attribute scores for each species trait for the 34 fish assemblages were regressed against the site scores on an index of hydrological variability derived from a principal components analysis of the eight hydrological variables using SYSTAT (Wilkinson 1989). A PCA was used because the principal components are derived solely from the hydrological data without reference to any grouping structure in the ecological data, as is the case with the CDA. A significant relationship (slope) between proportional occurrence of species traits and hydrological variability was taken as evidence that a particular trait was expressed along the hydrological gradient among the 34 sites. Again, the unprotected P values are reported for each of the regressions.

Zoogeographic constraints on fish assemblage structure.—A taxonomic analysis was performed to determine similarity of sites based on species composition. Groups of taxonomically similar assemblages were identified with two-way indicator species analysis (TWINSPAN, Hill 1979), a divisive hierarchical technique that is highly interpretable because it places the most similar samples together in the dendrogram's sample sequence (Gauch 1982:201). TWINSPAN has been widely used as a classification tool for ecological communities, including those in streams (see Norris and Georges 1993).

Possible confounding factors.—We evaluated the extent to which additional factors not included in the analysis might confound any observed patterns. We explored several aspects of the data, including variation in sampling intensities, stream sizes, and species/area relationships. We also considered the extent to which our classification results might be explicable in terms of regional-scale features such as ecoregion designation (Omernik 1987).

RESULTS

The available hydrological record for the 34 sites ranged from 21 to 55 yr, with a median of 45 yr (Appendix 1). The eight hydrological variables exhibited a wide range of values. Daily flow coefficient of variation showed the greatest range in values, although daily flow predictability, baseflow stability, and low-flow predictability also exhibited wide variation across sites.

A total of 106 fish species was represented across the 34 sites (Appendix 2). Only one species (*Luxilus cornutus*) occurred at all 34 sites; four others were recorded at ≥ 30 sites (*Catastomus commersoni, Etheostoma nigrum, Pimephales notatus, Semotilus atromaculatus*). A total of 15 species occurred at ≥ 20 sites, while 66 species were found at 10 or fewer sites. Twenty species were recorded at only one of the 34 sites.

TABLE 2. Summary of canonical discriminant analysis (CDA) for two ecological groups defined in terms of functional species traits. Group means and standard deviation (in parentheses) are given for each hydrologic variable, as are univariate F statistics and associated P values, which indicate whether the groups differ with respect to individual variables. Total canonical structure coefficients for the canonical variate indicate correlations between the canonical variate and the original hydrologic variables. Mean scores for each functionally defined group are given for each canonical variate.

	Hydrologically variable sites	Hydrologically stable sites	$F_{1,32}$	P	Correlation with canonical variate*
N	16	18			
Daily flow predictability	46.5 (19.9)	67.7 (11.1)	15.08	0.001	0.834
Baseflow stability	0.16 (0.19)	0.32 (0.17)	6.78	0.01	0.616
Daily flow coefficient of variation	173.5 (73.7)	137.2 (60.7)	2.48	0.12	−0.395
Frequency of spates	0.75 (0.17)	0.67 (0.08)	2.68	0.11	−0.410
Group mean on canonical variate	−0.951	0.850			

* Squared canonical correlation ($=R^2$) between canonical variate and all hydrologic variables = 0.46 ($F_{4,29}$ = 6.19, P = 0.001).

For individual sites, the range of species collected ranged from 21 to 51, with a median of 31 (Appendix 1). Sampling intensity also varied among the sites, with the number of collections falling within a 15 km radius of the gauge ranging from 1 to 40, with a median of 7 (Appendix 1).

Functional attribute scores were derived for most of the 106 species. Missing values occurred for morphological features (1 species), substratum preference (2 species) and tolerance to silt (15 species) (see Appendix 2). Some attributes were significantly cross correlated (Appendix 3), an expected result that was addressed by use of multivariate analytical techniques.

Hydrological correlates of fish assemblage functional structure

When ecological similarity among sites was defined in terms of functional attributes, various numbers of groups of similar sites were identified using hierarchical classification. The canonical discriminant analysis was able to successfully distinguish two groups solely in terms of the independent hydrological variables. When more than two groups were specified, the explanatory power of additional canonical variates was low. Because four hydrological variables were the most important in distinguishing among the groups, it was advantageous to restrict the number of ecologically defined groups to two in order to maintain the 3:1 ratio of group size to explanatory variables, as advised by Williams and Titus (1988).

Assemblages at the 34 sites were separated into two functionally defined clusters consisting of 16 and 18 sites. The CDA derived linear combinations of the eight hydrological variables to discriminate among the two groups. Four variables were heavily weighted ($F > 2.0$) in the initial CDA and were subsequently retained (Table 2). Univariate F tests indicated that daily flow predictability ($P < 0.001$) and baseflow stability ($P = 0.01$) were highly significant, while daily flow coefficient of variation ($P = 0.12$) and frequency of spates ($P = 0.11$) were not significant but had some discriminatory power. Overall, the canonical variate was highly significantly different from zero (squared multiple correlation = 0.46, $P = 0.001$), indicating that the four hydrological variables successfully discriminated the two ecological groups.

Correlations between the canonical variate and the original hydrological variables showed that the canonical variate represents a contrast between flow stability (high positive correlation with daily flow predictability and baseflow stability) vs. flow variability (negative correlation with daily flow coefficient of variation and spate frequency). Mean group scores on this variate indicated that assemblages in Group 1 ($\bar{X} = -0.95$) are associated with hydrologically variable sites, while assemblages in Group 2 ($\bar{X} = 0.85$) are associated with hydrologically stable sites. Fig. 1 summarizes graphically these results by showing that the canonical variate separates assemblages into hydrologically "variable" sites and hydrologically "stable" sites.

Discriminant function analyses correctly classified the sites into prior ecological groups based only on the four hydrological variables with 85% accuracy. Proper classification was higher for the hydrologically stable sites (17/18) than for the hydrologically variable sites (12/16). The geographic distribution of the functionally similar groups is shown in Fig. 2.

Ecological organization of functionally similar assemblages

Several consistent patterns emerged when the functional composition of fish assemblages was contrasted with corresponding hydrological characteristics. We investigated the relative contributions of the various functional attributes to defining the ecologically similar groups by plotting group means and standard errors and performing *t* tests.

Marked differences in trophic organization existed among the 34 sites in accordance with hydrological regime (Fig. 3a). Stable sites had more benthic invertivores ($P < 0.0001$) and fewer omnivores ($P < 0.001$) and generalist invertivores ($P = 0.07$). Stable sites also had fewer planktivores ($P = 0.01$) but more parasitic fishes ($P = 0.06$), although both these groups were poorly represented at all sites (Fig. 3a). In general, these patterns suggest that generalist trophic strategies are associated with hydrological variability in these streams.

For stream size association (Fig. 3b), fish assemblages from variable streams had proportionately more species characteristic of small streams ($P = 0.06$) and of lentic waters ($P = 0.06$) and proportionately fewer medium to large river species ($P < 0.001$) than did assemblages from stable streams.

For water velocity preference (Fig. 3c), assemblages from stable streams had proportionally more fast-velocity fishes ($P < 0.0001$) and medium-velocity fishes ($P = 0.004$) than did those from variable streams, which contained more slow-velocity species ($P < 0.0001$). Proportions of fishes with general water velocity preferences were similar among groups but tended to be greater in stable streams ($P = 0.08$).

For substratum preference (Fig. 3d), assemblages in variable streams had proportionately fewer species associated with rubble ($P < 0.0001$) but more species typically associated with silt ($P < 0.0001$) compared to stable stream assemblages. Substratum generalists tended to be more prevalent in variable streams ($P = 0.08$), while species associated with sand were not differentially represented between the variable and stable stream assemblages ($P > 0.4$).

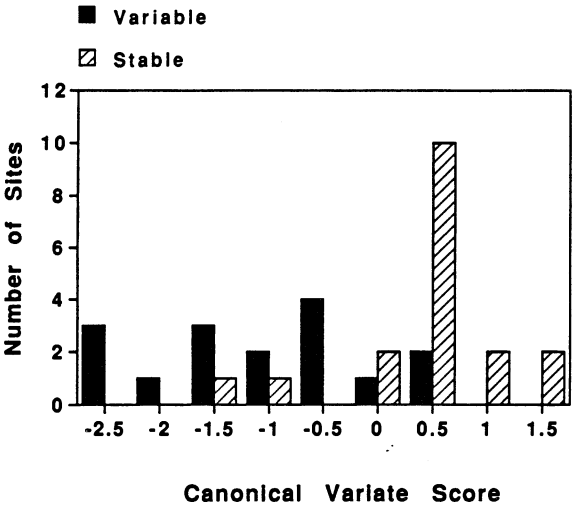

FIG. 1. Classification of 34 individual Wisconsin and Minnesota sites into hydrologically variable and hydrologically stable groups based on canonical variate scores when assemblages are defined in terms of species functional attributes. Negative canonical variate scores are correlated with daily flow coefficient of variation and spate frequency, while positive canonical scores are correlated with daily flow predictability and baseflow stability (see Table 2).

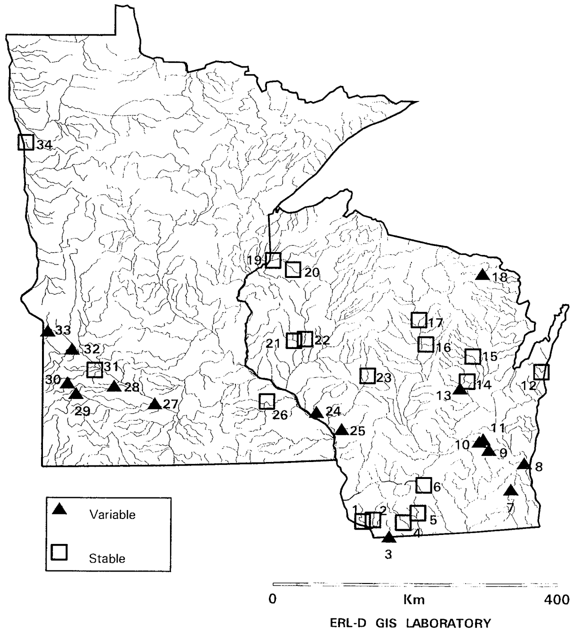

FIG. 2. Geographical locations of 34 sites, coded by group membership based on functional description of fish assemblages. Numbers 1–34 indicate sites described in Appendix 1. ERL-D GIS is the Environmental Research Laboratory-Duluth Geographical Information System Laboratory.

Proportional representation of species differentially tolerant to silt varied substantially among the two groups of assemblages. Stable sites had fewer silt-tolerant species ($P < 0.0001$) and species of moderate tolerance ($P = 0.02$), while variable sites had more tolerant species ($P < 0.0001$).

The morphological variables used in the analysis showed mixed results. No differences were found for the swimming factor for the variable sites (mean ± 1 SE = 0.553 ± 0.017) vs. the stable sites (0.556 ± 0.018). By contrast, relatively large differences in the shape factor ($P = 0.03$) were observed between the variable sites (4.994 ± 0.057) and the stable sites (5.213 ± 0.075).

Several species of fish showed distinct affiliation with sites of differing hydrology. Species that occurred at ≥50% of the stable sites but ≤50% of the variable sites were *Moxostoma macrolepidotum, Micropterus dolomieu, Hypentelium nigricans, Rhinichthys cataractae,* and *Notropis rubellus* (see Appendix 2). Species occurring at ≥50% of variable sites but ≤50% of stable sites were *Ameiurus melas, Perca flavescens, Notemigonus crysoleucas, Ameiurus natalis,* and *Lepomis gibbosus.* Several species occurred at ≥50% of both variable and stable sites. They were *Catostomus commersoni, Luxilus cornutus, Semotilus atromaculatus,*

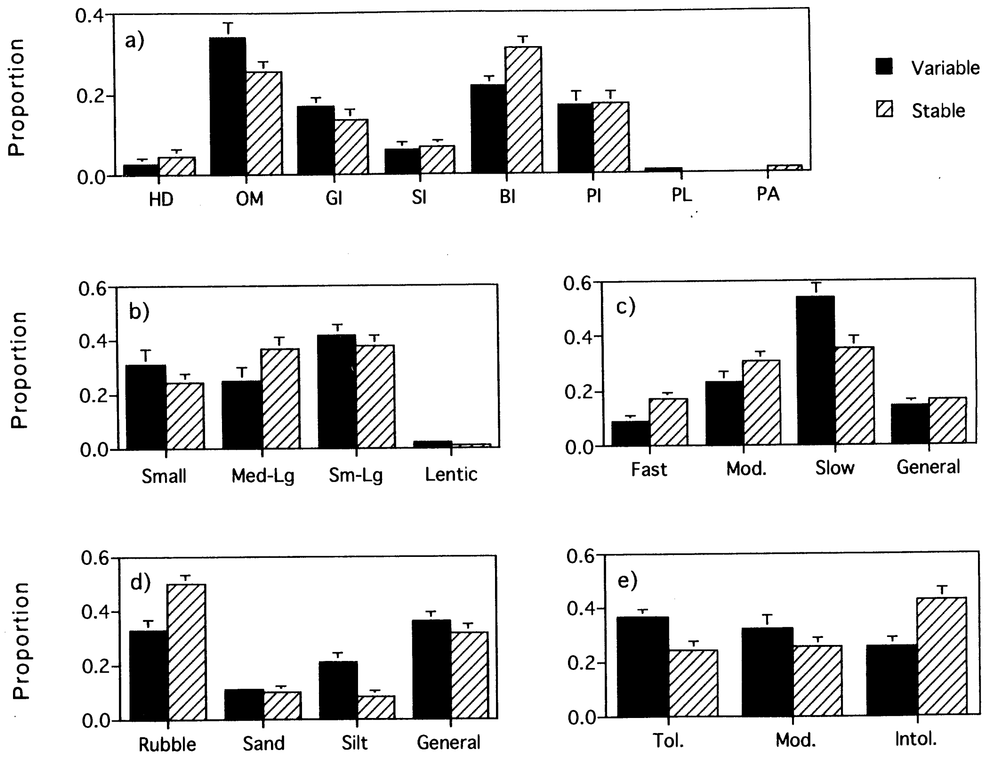

FIG. 3. Mean proportions (+ 2 SE) for functional attributes of assemblages from 34 sites divided into two groups (see Table 1 for definitions). (a) Trophic guild (HD = herbivore-detritivore, OM = omnivore, GI = general invertivore, SI = surface/water column invertivore, BI = benthic invertivore, PI = piscivore-invertivore, PL = planktivore, PA = parasite), (b) stream size preference, (c) current velocity preference, (d) substratum preference, (e) silt tolerance.

Etheostoma nigrum, Pimephales notatus, Cyprinella spiloptera, Cyprinus carpio, Nocomis biguttatus, Notropis stramineus, Pimephales promelas, Esox lucius, Noturus flavus, and *Percina maculata.*

Ecological organization and hydrological gradients

To examine changes in functional organization of fish assemblages along a gradient of hydrological stability among streams, species trait scores for fish assemblages were regressed on an index of hydrological variability derived from a PCA for all 34 sites. The first three principal components described 42, 22, and 19% of the total hydrological variation, respectively. Hydrological variables having high loadings on the first component were predictability of daily flow (0.924), baseflow stability (0.964), and coefficient of variation of daily flows (−0.873). Spate frequency had a moderate loading (−0.524) on the first component. Thus, the first component represents a contrast between sites having hydrological variability vs. hydrological stability, and is very similar to the canonical variate derived in the CDA (correlation between site scores for the canonical variate and the first principal component = 0.59). Site scores on this first principal component were used as an index of hydrological stability for a simple linear regression analysis (Table 3). Addition of the second and third principal components in a multiple linear regression did not result in a general improvement of variation explained; therefore, they were omitted from the regression analysis.

Along a gradient of increasing hydrological stability across sites, there were substantial decreases in omnivory ($P < 0.001$) and general invertivory ($P = 0.01$) and large increases in piscivory ($P < 0.001$), parasitism ($P = 0.01$), and benthic invertivory ($P = 0.09$). The proportion of small stream fishes declined ($P = 0.002$) across this gradient while the number of lentic species tended to increase ($P = 0.11$). As hydrological stability increased, greater proportions of fishes typified by moderate water velocities occurred ($P = 0.05$), and smaller proportions of slack water species occurred ($P = 0.08$). Fishes associated with coarse rubble substrata tended to increase with increasing stability ($P = 0.10$), while species preferring silt declined ($P = 0.03$). As stability increased, the proportion of silt-intolerant species increased ($P = 0.002$), while the proportion of silt-tolerant species declined ($P = 0.001$). Finally, along a gradient of hydrological stability, the proportion of elongate fishes increased ($P = 0.03$). In general, these results are similar to those discerned from the CDA using the two ecological groups (cf. Table 3 with Fig. 3).

TABLE 3. Summary of statistics for separate regressions of 25 functional attribute scores (composite score for each fish assemblage) vs. an index of hydrologic stability (first principal component scores) for 34 sites. The sign of the slope indicates how an individual trait changes as hydrologic stability increases across sites. Bold-faced species traits indicate nonzero slopes (unprotected P values ≤ 0.05, df = 32).

	Slope	SE	r	t statistic	P
Trophic guild					
Herbivore-detritivore	0.007	0.006	0.214	1.236	0.225
Omnivore	−0.047	0.011	−0.598	−4.219	0.000
General invertivore	−0.023	0.009	−0.420	−2.620	0.013
Surface/water column invertivore	−0.003	0.007	−0.090	−0.512	0.612
Benthic invertivore	0.021	0.012	0.299	1.775	0.085
Piscivore	0.037	0.009	0.604	4.291	0.000
Planktivore	0.000	0.002	0.042	0.056	0.815
Parasite	0.007	0.003	0.439	2.766	0.009
Stream size preference					
Small	−0.049	0.015	−0.508	−3.332	0.002
Medium-large	0.022	0.019	0.204	1.180	0.108
Small-large	0.022	0.014	0.266	1.561	0.128
Lentic	0.006	0.003	0.279	1.644	0.110
Current velocity preference					
Fast	0.006	0.010	0.107	0.608	0.548
Moderate	0.028	0.014	0.338	2.031	0.050
Slow-none	−0.040	0.023	−0.300	−1.781	0.084
General	0.006	0.007	0.155	0.890	0.380
Substratum preference					
Rubble	0.034	0.020	0.289	1.710	0.097
Sand	−0.008	0.007	−0.187	−1.078	0.289
Silt	−0.032	0.014	−0.376	−2.299	0.028
General	−0.001	0.013	−0.015	−0.085	0.933
Tolerance to silt					
High	−0.056	0.012	−0.648	−4.808	0.000
Moderate	−0.025	0.015	−0.278	−1.637	0.111
Low	0.060	0.018	0.507	3.325	0.000
Body morphology					
Swim factor	−0.006	0.012	0.084	−0.476	0.637
Shape factor	0.108	0.049	0.365	2.218	0.034

Zoogeographic constraints on fish assemblage structure

The TWINSPAN analysis identified four groups of sites that show a clear regional clustering (Fig. 4). TWIN 1 sites tend to occur along the Lake Michigan shore of Wisconsin; TWIN 2 sites are located in northern, interior Wisconsin; TWIN 3 sites are almost entirely restricted to Minnesota; and TWIN 4 sites are restricted to southwestern Wisconsin. The hierarchical nature of the analysis allows the four identified groups to be coalesced into two larger but taxonomically related groups. TWIN 1+2 and TWIN 3+4 can be combined in this way to produce one cluster of eastern and northern-interior Wisconsin streams (all circles in Fig. 4), and another cluster of western Wisconsin and Minnesota streams (all squares in Fig. 4).

If species distributions could explain the observed relationships between stream hydrology and the functional organization of fish assemblages, we would expect to see the geographic distribution of taxonomically similar sites corresponding to the distribution of functionally similar sites. We addressed this by comparing the geographic distributions of the combined TWIN 1+2 groups and the TWIN 3+4 groups (Fig. 4) with the geographic distributions of the variable and stable sites (Fig. 2). Inspection of these two figures reveals that the 17 taxonomically similar TWIN 1+2 sites consist of a mix of 7 hydrologically variable and 10 hydrologically stable sites. Likewise, the 17 taxonomically similar TWIN 3+4 sites consist of a mix of 9 variable and 8 stable sites. This lack of correspondence indicates that the hydrological correlates of functional organization of fish assemblages in the 34 sites cannot be explained in terms of zoogeographic constraints emerging at the regional scale.

Possible confounding factors

The potential confounding of these hydrological–ecological relationships by sampling intensity and catchment area was assessed by examining whether the identified groups of sites differed with respect to these factors. Groups of sites did not differ significantly from one another in terms of average species number (t_{32} = 0.51, P = 0.6), logarithm of sample size (t_{32} = 1.4, P

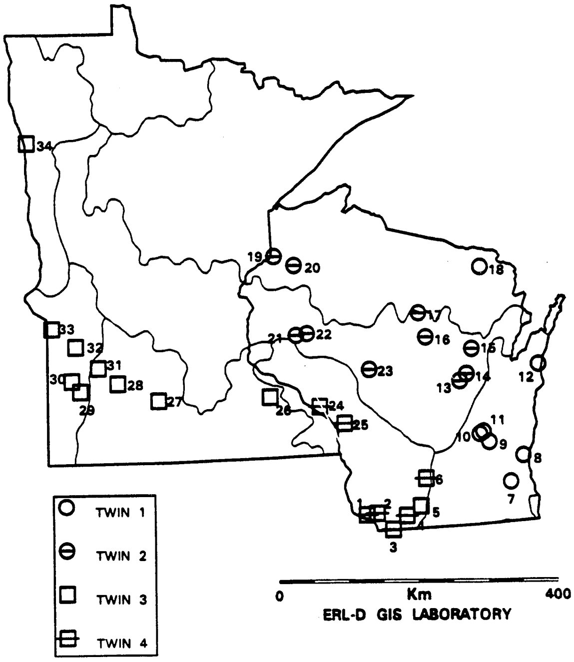

FIG. 4. Geographical locations of 34 sites grouped according to taxonomic affiliation defined in four-group TWINSPAN classification. Ecoregion boundaries (Omernik 1987) are also indicated. Numbers 1–34 indicate sites described in Appendix 1. ERL-D GIS is the Environmental Research Laboratory–Duluth Geographical Information System Laboratory.

= 0.2), or logarithm of catchment area ($t_{32} = -1.04$, $P = 0.3$). However, there were some strong relationships among these variables. Groups of functionally similar sites expressed a strong relationship between number of species collected and sampling intensity at each site (Fig. 5a). The linear relationship between species number and the logarithm of sample number was significant for both variable sites (slope = 19.1, SE = 5.3, $r = 0.70$, $F_{1,14} = 12.8$, $P = 0.003$) and stable sites (slope = 20.9, SE = 4.1, $r = 0.79$, $F_{1,14} = 25.9$, $P < 0.001$), but the groups did not differ from one another (ANCOVA for homogeneity of slopes: $F_{1,30} = 0.07$, $P = 0.8$). There was no significant relationship between number of species collected and logarithm of catchment area ($P > 0.2$ for both groups); however, there was an increase in the maximum number of species recorded for a given catchment area as catchment area increased (Fig. 5b), as has been observed elsewhere (Fausch et al. 1984). Fig. 5c shows that there is a significant relationship between species per unit area (log scale) and sampling intensity for both variable sites (slope = 7.6, SE = 1.3, $r = 0.83$, $F_{1,14} = 31.7$, $P < 0.001$) and stable sites (slope = 9.3, SE = 1.5, $r = 0.84$, $F_{1,16} = 36.8$, $P < 0.001$), but these two groups do not differ in terms of their responses (ANCOVA for homogeneity of slopes: $F_{1,30} = 0.75$, $P = 0.4$). In short, these analyses indicate that, although sampling intensity is an important covariate influencing patterns of species richness across a range of catchment sizes, neither differential sampling intensity nor catchment area alone can explain differences in functional organization for the two ecologically similar groups used in the analysis.

Omernik (1987) divided the United States into ecoregions, areas of similar landsurface form, soils, and land use. Some studies have shown correspondence between fish assemblage structure and ecoregion boundaries (Lyons 1989), while others have not (Hawkes et al. 1986). If ecoregions fully explained the distribution of the sites, we would expect to see taxonomically or functionally defined groups restricted to particular ecoregions. Six ecoregions in Wisconsin and Minnesota con-

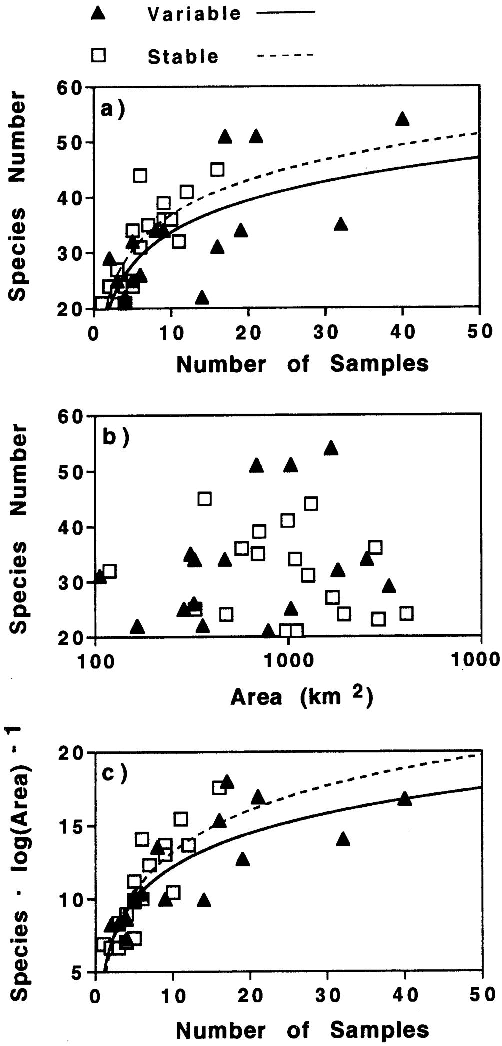

FIG. 5. Among-site relationships among 34 sites coded by two functionally similar groups for (a) number of survey samples vs. species collected, (b) catchment area vs. species number, and (c) number of samples vs. number of species per unit catchment area (defined on $\log_{10}$ scale). Slopes for two groups are not significantly different from one another in either (a) or (c).

tain at least three sites. The distribution of the four taxonomically similar groups shows very clear geographic patterns relative to these six ecoregions (Fig. 4). The taxonomic structure of the stream fish assemblages from the 34 sites is highly predictable from knowledge of ecoregion designation (cf. Lyons 1989). Further, if only two taxonomic groups (TWIN 1+2 and TWIN 3+4) are considered, each of the six ecoregions contains exclusively either one group or the other. By contrast, the functionally defined assemblages are not as regularly distributed among the six ecoregions (Fig. 2). Only one ecoregion (in extreme southwestern Minnesota) contains exclusively variable sites; all other ecoregions contain assemblages characteristic of both variable and stable hydrological regimes. This pattern indicates that the geographic distribution of functionally defined assemblages is not entirely predictable from ecoregion designations. However, there is some geographic pattern in the distribution of functionally defined sites, with variable sites tending to occur in southeastern Wisconsin and southwestern Minnesota, and stable sites tending to occur in southwestern and north-central Wisconsin. While this pattern suggests that some ecoregions are more similar than others in terms of functional composition of fish communities, it indicates that these similar ecoregions need not be geographically contiguous, in contrast to the among-ecoregion pattern observed when assemblages were viewed in terms of taxonomic similarity (cf. Figs. 2 and 4).

Discussion

This analysis documents strong associations between both functional and taxonomic composition of fish assemblages and hydrological regimes at a regional scale. Many previous studies have related the taxonomic structure of fish assemblages to habitat (e.g., Gorman and Karr 1978, Schlosser 1985, 1987, Angermeier 1987, Bozek and Hubert 1992, Nelson et al. 1992) and to hydrological variation, particularly floods (e.g., Harrell 1978, Meffe 1984, Schlosser 1987, Jowett and Duncan 1990). Of the very few that have related stream fish community structure to long-term hydrological variability across many streams (Horwitz 1978, Fausch and Bramblett 1991), none have examined the functional organization of fish assemblages (but see Bain et al. 1988 for a functional comparison of two streams). Our findings for 34 sites, by contrast, suggest that hydrological factors explain variation in the functional organization of stream fish assemblages, at least when viewed in terms of species presence/absence. These patterns can be generalized across zoogeographic domains and may have important implications for community assembly and food web structure in streams.

The patterns documented here, taken as a whole, are consistent with the general theoretical expectation that environmentally variable lotic ecosystems contain more trophic and habitat generalists and more tolerant species than do stable systems (cf. Poff and Ward 1989). Fish assemblages can be associated with hydrologically "variable" and "stable" sites (Fig. 3), or they can be arrayed along a gradient of hydrological stability (Table 3). Either of these approaches yields results showing that assemblages from hydrologically variable streams have generalized feeding strategies, are associated with silt and general substrata, are characterized by slow-velocity species with headwater affinities, and are tolerant to silt. By contrast, stable streams have more species that are silt-intolerant, trophic specialists and are associated with fast or moderately flowing and/or permanent streams. While these broad differences in functional organization reflect differences in species composition across the sites (Appendix 2), they cannot be explained solely in terms of regional zoogeographic or ecoregion constraints.

The finding that assemblages from hydrologically variable streams contain more small-stream and wide-ranging species (Fig. 3b) offers an intriguing possible interpretation. One might expect hydrologically variable sites to be comprised of "colonizing" species that Schlosser (1987) identified as adapted to unstable headwaters of temperate warmwater streams of the central United States. Interestingly, the variable sites in this study span the entire range of stream sizes in the data set (Fig. 5b), suggesting that large streams may function like "headwater" streams if they experience significant seasonal hydrological variability, which would serve to reduce habitat volume.

The absence of a strong species–area relationship for the range of stream sizes examined suggests a potential limitation of this study, because species–area relations have been documented in many systems (e.g., Fausch et al. 1984, Watters 1992). In a study of midwestern streams, Fausch et al. (1984) found that maximum species richness increased with increasing catchment area, but many larger streams had fewer species than would be expected based on species–area relations. They concluded that low species richness at sites of large area can be due to poor sampling, degradation, or natural variability in species richness. In the present study, the smaller streams were "sampled" (i.e., survey collections ≤15 km from the stream gauge) more frequently than larger streams, thus obscuring any species–area relationship (Fig. 5b). Given the strong relationship between sampling intensity, species collected, and catchment area in this study, we suspect that a clearer species–area relation would exist for the sites had all sites been sampled with equal relative effort. However, the fact that similar species–area and species–sampling intensity relationships were found for the identified assemblages supports the argument that the hydrological–ecological patterns documented here are not simply artifacts of differential sampling effort. A point worth emphasizing is that species–area relationships may themselves reflect hydrological variability. For example, in some north temperate streams, mobile opportunists may continually move into and out of available habitats as physical conditions change (Angermeier and Schlosser 1989), thus potentially obscuring species–area relations. The question of the relationship between species–area curves and hydrological variability deserves closer attention.

We were able to document differences in the taxonomic and functional organization of stream fish assemblages in relation to hydrological regime despite several shortcomings in the data. This outcome reflects a number of important factors. First, streams in this region are speciose. The 106 species represented in the data set provide a wide range of functional attribute variation that facilitates the detection of species–environment patterns. Second, the 34 gauged streams included in the analysis represent a relatively wide range of hydrological regimes for such a small geographic area. Of the 10 or so classes of streamflow regimes of putative ecological interest identified by Poff and Ward (1989) and Poff and Allan (1993) for U.S. streams, 6 occurred in the data set. Discrimination among ecological assemblages based on hydrological factors would likely be more difficult in a region characterized by narrow hydrological variation or species-poor faunas (e.g., see Persat et al. 1994).

A third contributing factor is that differences between variable and stable hydrological designations in these midwestern streams probably reflect differences in other, similarly important environmental factors, especially thermal regime and habitat volume. For example, Coon (1987) found hydrological differences between two sites on a Minnesota river and observed that the more variable site experienced greater flow fluctuations including low summer baseflow conditions, more rapid response to storm runoff, and much lower winter temperatures that allowed extensive ice cover to develop. These observations suggest a correlation between flow variability and seasonal disturbance intensity that may hold for the midwestern streams considered in this paper. Stream fish assemblages can be influenced both by physiologically stressful warm-weather oxygen depletions (see Matthews 1987) and extensive winter ice cover (Schlosser 1987). The very stable hydrological sites in this study likely are characterized by high groundwater inflow and relatively sparse ice cover in winter and minimal oxygen stress in summer. By contrast, the variable hydrological sites are likely to present relatively harsh conditions in terms of winter ice and low summer water velocities, with associated seasonal thermal/oxygen stress and fluctuations in habitat volume. Similar physical correlates have been observed for New Zealand streams in relation to hydrological variability (Jowett and Duncan 1990). These observations underscore the importance of hydrological regime as an integrator of many significant environmental constraints.

A final factor that probably contributes to the strong patterns revealed is the appropriate "scaling" of the hydrological and ecological data. Because fish are relatively mobile and long lived, large spatial and temporal scales may be required to adequately describe fish assemblage structure. Rapid recolonization of vacated stream reaches by fish is well documented (e.g., Larimore et al. 1959, Peterson and Bayley 1993), as are shifts in assemblage structure between years under changed hydrological conditions (Ross et al. 1985). Thus, whole-system hydrology may be a reasonable index of habitat suitability for fishes when viewed at a broad regional scale. Given the constraints of the data sets, we were forced to conduct a very coarse-grain analysis, so the scaling was in some sense fortuitous. However, the characterization of the fish assemblage data in terms of species traits represented a further "coarsening" of the binary taxonomic data that revealed more general and complementary patterns. This functional approach, combined with species presence/absence data and long-term average measures of hydrological factors, probably facilitated detection of coarse-grain patterns. In all likelihood, more detailed hydrological information would be needed to detect fine-grained ecological patterns such as interannual variation in population abundances or size structure (e.g., Strange et al. 1992). Similarly, finer grained (site-specific and temporal) descriptions of environmental variability might be required to determine hydrological constraints on more sedentary assemblages with higher turnover rates, such as lotic invertebrates and algae (cf. Townsend and Hildrew 1994).

The use of species traits data to describe differences in assemblage structure across differentially variable environments provides some corroboration for Southwood's (1977, 1988) "habitat templet" hypothesis, which a number of authors have suggested is particularly relevant for lotic ecosystems (Schlosser 1987, 1990, Minshall 1988, Poff and Ward 1989, 1990, Poff 1992*a*, Townsend and Hildrew 1994). Our results suggest that certain hydrological factors, particularly fluctuations in baseflow, can indicate habitat persistence for fish and thus provide information on the suite of species traits (and corresponding species) most likely to be favored under a particular hydrological regime in a given zoogeographic region. By implication, modifications of hydrological regimes should lead to adjustments in coarsely defined assemblage structure. For example, climate change is expected to alter precipitation–runoff regimes, thereby potentially modifying community structure in streams across entire regions (Grimm 1992, Poff 1992*b*). Detecting assemblage responses to such broad-scale change would probably be facilitated by use of functional species traits, which can be generalized across taxonomically defined zoogeographic domains. Indeed, generalist and tolerant species are expected to benefit from climate change (Tonn 1990), in part because they are better able to invade new habitats (Holdgate 1986). Similarly, specialist fish species that invade temporally variable habitats may neither persist (Meffe 1984) nor modify assemblage structure of the invaded habitat (Zaret 1982). Increasing hydrological variability associated with climate change (or other anthropogenic modifications, such as impoundment) can be expected to modify habitat templates, thereby changing the relative value of species traits that promote local persistence (cf. Bain et al. 1988, Scarnecchia 1988). Over time, discernible shifts in assemblage structure would be expected.

Hydrological regime can be used as a proxy to coarsely define lotic fish assemblage composition in northern Midwestern streams. Of course, hydrological regime alone cannot fully explain patterns in assemblage structure, because other important habitat features are known to have local influence independent of discharge (e.g., habitat complexity). The importance of other physical habitat factors has been amply documented in the literature (e.g., Gorman and Karr 1978, Angermeier 1987, Pearsons et al. 1992). Nonetheless, at regional (among-stream) scales, our results indicate that a substantial and ecologically interesting portion of variation in stream fish assemblage structure is associated with whole-system hydrological variables, a result that provides a basis for future, finer grained research.

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APPENDIX 1

Sampling characteristics, fish assemblage classifications, and summary of hydrologic variables of 34 Wisconsin and Minnesota sites. Given for each site are the map number (see Figs. 2 and 4), the USGS gauge number, the stream name, catchment area, the number of species combined across all collections since 1960, the number of individual samples at a site since 1960, the years in which fish data were available, the period of available hydrologic data, the functional group

Map no.	USGS gauge no.	Stream name	Area (km²)	No. spp.	No. samp.	Fish record	Hydrol. record
10	05423500	S. Br. Rock R.	165	22	14	1971–1977	1949–1969
11	05423000	W. Br. Rock R.	105	31	16	1971–1989	1950–1970
29	05315000	Redwood R.	785	21	4	1973–1986	1941–1985
32	05300000	Lac Qui Parle R.	2546	34	9	1960–1987	1934–1985
7	05543830	Fox R.	326	34	8	1971–1978	1964–1986
33	05293000	Yellow Bank R.	1031	25	3	1969–1985	1940–1985
28	05316500	Redwood R.	1805	32	5	1960–1986	1936–1985
31	05313500	Yellow Medicine R.	1691	27	3	1960–1976	1940–1985
9	05424000	E. Br. Rock R.	469	34	19	1971–1989	1950–1970
30	05311400	S. Br. Yellow Medicine R.	288	25	5	1973–1987	1961–1981
6	05406500	Black Earth Cr.	118	32	11	1966–1988	1955–1986
25	05383000	La Crosse R.	1031	51	21	1966–1982	1929–1970
8	04086500	Cedar Cr.	311	35	32	1963–1989	1931–1970
27	05317000	Cottonwood R.	3315	29	2	1962–1975	1939–1985
13	04081000	Waupaca R.	686	51	17	1960–1979	1929–1963
20	05332500	Namekagon R.	1264	31	6	1976–1981	1929–1970
19	05333500	St. Croix R.	4092	24	2	1976–1977	1929–1981
18	04063700	Popple R.	360	22	4	1965	1964–1986
21	05368000	Hay R.	1083	34	5	1962–1976	1951–1986
24	05379500	Trempealeau R.	1665	54	40	1963–1979	1935–1986
5	05433000	E. Br. Pecatonica R.	572	36	9	1960–1976	1940–1986
22	05367500	Red Cedar R.	2823	36	10	1973–1988	1929–1961
3	05415000	Galena R.	324	26	6	1970–1979	1940–1986
12	04085200	Kewaunee R.	329	25	5	1962–1973	1967–1986
23	05381000	Black R.	1940	24	5	1968–1977	1929–1986
17	05394500	Prairie R.	477	24	4	1976–1988	1940–1986
4	05432500	Pecatonica R.	707	39	9	1960–1986	1940–1986
15	04078500	Embarrass R.	995	41	12	1973–1980	1929–1985
34	05069000	Sand Hill R.	1103	21	1	1976	1948–1983
14	04080000	Little Wolf R.	1313	44	6	1972–1981	1929–1970
2	05414000	Platte R.	368	45	16	1962–1978	1935–1986
16	05397500	Eau Claire R.	971	21	4	1961–1989	1940–1986
1	05413500	Grant R.	697	35	7	1962–1978	1935–1986
26	05374000	Zumbro R.	2927	23	3	1963–1967	1931–1980

APPENDIX 1. Continued.

designation of the combined assemblage (1 = hydrologically variable, 2 = hydrologically stable), the taxonomic group designation of the combined assemblage (TWINSPAN group), the canonical variate scores, and the values for the eight individual hydrologic factors. Sites are ordered according to ranked canonical variate scores, which represent a gradient from hydrological variability (negative scores) to stability (positive scores).

Funct. group	Taxon. group	Canonical score	Daily flow coeff. var.	Daily flow predict.	Spate freq.	Spate predict.	Spate-free period	Baseflow stability	Lowflow predict.	Lowflow-free period
1	1	−2.49	205.2	27.29	0.86	0.53	0.23	0.02	0.50	0.46
1	1	−2.23	196.6	26.9	0.95	0.65	0.35	0.04	0.50	0.51
1	3	−2.14	204.1	28.4	0.78	0.75	0.61	0.02	0.54	0.39
1	3	−1.75	236.2	24.0	0.87	0.79	0.59	0.01	0.48	0.30
1	1	−1.45	112.6	55.2	0.57	0.64	0.37	0.13	0.71	0.59
1	3	−1.36	257.1	28.7	0.76	0.61	0.50	0.02	0.60	0.35
1	3	−1.36	201.5	32.5	1.06	0.56	0.28	0.02	0.39	0.38
2	3	−1.26	231.9	34.0	0.70	0.67	0.59	0.02	0.50	0.41
1	1	−0.94	168.0	46.8	0.81	0.55	0.19	0.05	0.80	0.57
1	3	−0.73	321.9	25.0	0.67	0.62	0.54	0.00	0.48	0.21
2	4	−0.55	68.1	69.8	0.66	0.54	0.28	0.60	0.36	0.28
1	4	−0.43	60.4	74.1	0.60	0.48	0.31	0.48	0.47	0.18
1	1	−0.37	186.7	45.7	0.88	0.64	0.37	0.08	0.39	0.29
1	3	−0.26	192.9	45.3	0.89	0.63	0.32	0.05	0.29	0.16
1	2	−0.17	44.5	74.7	0.57	0.79	0.23	0.55	0.34	0.27
2	2	0.22	39.9	78.6	0.74	0.58	0.41	0.51	0.47	0.35
2	2	0.22	54.2	78.5	0.60	0.61	0.54	0.53	0.35	0.21
1	1	0.45	103.6	73.5	0.43	0.75	0.45	0.24	0.63	0.37
2	2	0.56	103.9	74.0	0.58	0.58	0.22	0.48	0.57	0.39
1	4	0.64	93.5	74.1	0.60	0.71	0.24	0.46	0.43	0.39
2	4	0.73	121.1	69.8	0.70	0.60	0.30	0.47	0.54	0.19
2	2	0.85	84.9	74.3	0.73	0.73	0.44	0.37	0.53	0.33
1	4	0.88	191.4	62.4	0.66	0.46	0.29	0.34	0.30	0.15
2	1	0.90	211.1	58.5	0.50	0.73	0.29	0.14	0.57	0.53
2	2	0.90	230.8	53.1	0.76	0.52	0.38	0.04	0.55	0.35
2	2	0.94	97.1	75.9	0.68	0.60	0.42	0.38	0.38	0.35
2	3	0.97	155.3	67.7	0.60	0.64	0.42	0.34	0.42	0.23
2	2	0.98	102.7	73.7	0.70	0.68	0.35	0.25	0.56	0.44
2	3	0.98	212.2	55.9	0.58	0.81	0.69	0.10	0.50	0.45
2	2	1.00	95.8	76.0	0.62	0.72	0.24	0.34	0.48	0.32
2	4	1.06	161.4	67.5	0.77	0.40	0.17	0.37	0.62	0.34
2	2	1.40	146.3	71.7	0.60	0.71	0.44	0.22	0.40	0.27
2	4	1.88	174.6	68.4	0.85	0.55	0.14	0.41	0.41	0.23
2	3	1.94	178.3	70.7	0.74	0.53	0.42	0.17	0.58	0.51

APPENDIX 2

List of 106 fish species (by family) from 34 study sites, showing total number of sites where each species was collected, the proportional occurrence of each species at hydrologically variable (N = 16) and hydrologically stable (N = 18) sites, and functional attribute scores (SwF = swim factor, ShF = shape factor, TR = trophic guild, WM = water movement, SUB = substratum, SS = stream size, TOL = tolerance (see Table 2 for codes)). Missing values are indicated by ellipses.

Family Species name	Total sites	Variable sites	Stable sites	SwF	ShF	TR	WM	SUB	SS	TOL
Acipenseridae										
Acipenser fulvescens	1	0.000	0.056	0.227	6.800	5	2	1	3	...
Amiidae										
Amia calva	2	0.125	0.000	0.767	6.806	6	3	3	4	...
Anguillidae										
Anguilla rostrata	1	0.062	0.000	0.620	13.365	6	4	4	4	1
Atherinidae										
Labidesthes sicculus	4	0.125	0.111	0.413	8.153	4	3	4	8	3
Catostomidae										
Carpiodes carpio	5	0.125	0.167	0.392	4.120	1	3	3	3	2
Carpiodes cyprinus	10	0.375	0.222	0.377	3.056	5	3	3	3	2
Carpiodes velifer	3	0.062	0.111	0.488	3.264	1	3	2	3	2
Catostomus commersoni	33	0.938	1.000	0.388	5.552	5	4	4	4	1
Erimyzon sucetta	1	0.062	0.000	0.458	4.278	5	3	3	6	3
Hypentelium nigricans	16	0.188	0.722	0.477	6.000	5	1	1	8	3
Ictiobus bubalus	2	0.125	0.000	0.578	3.400	5	2	3	3	2
Ictiobus cyprinellus	5	0.188	0.111	0.536	3.457	3	3	4	3	2
Moxostoma anisurum	18	0.438	0.611	0.361	4.222	5	3	4	8	3
Moxostoma carinatum	1	0.000	0.056	0.459	4.822	5	2	1	3	3
Moxostoma erythrurum	19	0.438	0.667	0.400	5.000	5	2	1	8	3
Moxostoma macrolepidotum	21	0.312	0.889	0.435	5.076	5	4	1	8	3
Moxostoma valenciennesi	3	0.062	0.111	0.378	5.227	5	2	1	7	3
Centrarchidae										
Ambloplites rupestris	15	0.375	0.500	0.409	2.868	6	2	1	7	3
Lepomis cyanellus	18	0.625	0.444	0.547	2.976	3	3	4	4	1
Lepomis gibbosus	11	0.500	0.167	0.472	2.462	3	3	4	4	2
Lepomis humilis	9	0.375	0.167	0.472	2.803	3	3	3	2	1
Lepomis macrochirus	17	0.562	0.444	0.453	2.328	3	3	4	4	1
Micropterus dolomieu	20	0.312	0.833	0.377	3.902	6	2	1	2	3
Micropterus salmoides	11	0.438	0.222	0.438	3.824	6	3	4	3	2
Pomoxis annularis	5	0.250	0.056	0.428	3.159	6	3	3	3	1
Pomoxis nigromaculatus	12	0.375	0.333	0.341	2.842	6	3	4	2	2
Clupeidae										
Dorosoma cepedianum	4	0.250	0.000	0.376	3.083	7	3	3	3	1
Cottidae										
Cottus bairdi	6	0.125	0.222	0.437	5.105	5	4	1	1	3
Cyprinidae										
Campostoma anomalum	8	0.375	0.111	0.421	5.527	1	2	1	7	2
Campostoma oligolepis	10	0.125	0.444	0.476	5.294	1	2	4	2	...
Clinostoma elongatus	1	0.000	0.056	0.460	6.163	4	1	1	1	3
Couesius plumbeus	5	0.312	0.000	0.347	5.612	3	4	1	2	1
Cyprinella spiloptera	23	0.688	0.667	0.417	5.415	4	3	4	8	1
Cyprinus carpio	24	0.812	0.611	0.425	3.808	2	3	4	8	1
Hybognathus nuchalis	1	0.000	0.056	0.416	5.285	1	3	4	3	3
Luxilus chrysocephalus	1	0.062	0.000	0.340	4.195	2	3	4	2	2
Luxilus cornutus	34	1.000	1.000	0.459	4.947	2	4	4	4	2
Lythrurus umbratilis	2	0.125	0.000	0.400	5.058	2	3	3	7	1
Margariscus margarita	4	0.250	0.000	0.387	5.551	3	3	2	1	...
Macrohybopsis aestivalis	1	0.000	0.056	0.342	6.129	3	1	1	3	3
Macrohybopsis storeriana	1	0.000	0.056	0.340	5.771	3	3	1	4	3
Nocomis biguttatus	26	0.688	0.833	0.444	5.114	2	2	1	7	3
Notemigonus crysoleucas	8	0.500	0.000	0.377	4.019	2	3	3	6	1
Notropis atherinoides	14	0.500	0.333	0.350	5.968	4	3	2	3	2
Notropis blennius	6	0.188	0.167	0.430	4.850	3	3	1	3	...
Notropis dorsalis	20	0.562	0.611	0.388	5.784	3	2	2	1	...
Notropis heterolepis	6	0.250	0.111	0.378	6.851	2	3	4	2	3
Notropis hudsonius	7	0.250	0.167	0.329	5.057	2	3	2	3	3
Notropis nubilus	1	0.000	0.056	0.405	5.151	1	2	1	2	...

APPENDIX 2. Continued.

Family Species name	Total sites	Variable sites	Stable sites	SwF	ShF	TR	WM	SUB	SS	TOL
Notropis rubellus	14	0.188	0.611	0.342	6.089	3	1	1	2	3
Notropis stramineus	21	0.688	0.556	0.346	5.904	2	2	2	4	2
Notropis texanus	1	0.000	0.056	0.367	5.361	1	3	2	2	...
Notropis volucellus	5	0.062	0.222	0.388	5.550	2	4	4	2	3
Phenacobius mirabilis	8	0.125	0.333	0.372	5.909	1	1	1	2	2
Phoxinus eos	5	0.188	0.111	0.451	4.822	2	3	3	1	2
Phoxinus erythrogaster	9	0.250	0.278	0.514	5.343	2	4	1	1	3
Phoxinus neogaeus	1	0.062	0.000	0.405	5.181	3	3	3	4	...
Pimephales notatus	30	0.938	0.833	0.463	5.128	2	4	4	4	1
Pimephales promelas	24	0.938	0.500	0.428	3.692	2	3	3	1	1
Pimephales vigilax	4	0.188	0.056	0.351	5.305	2	3	4	4	1
Rhinichthys atratulus	18	0.625	0.444	0.454	6.000	2	1	1	1	2
Rhinichthys cataractae	16	0.250	0.667	0.500	6.068	5	1	1	4	3
Semotilus atromaculatus	33	1.000	0.944	0.405	5.222	2	2	1	1	1
Esocidae										
Esox americanus vermiculatus	1	0.062	0.000	0.315	7.000	6	3	3	4	2
Esox lucius	24	0.812	0.611	0.343	7.121	6	3	4	8	3
Esox masquinongy	1	0.000	0.056	0.382	6.875	6	2	1	8	3
Cyprinodontidae										
Fundulus notatus	1	0.062	0.000	...	...	4	3	4	4	1
Gadidae										
Lota lota	8	0.125	0.333	0.456	7.571	6	2	1	8	...
Gasterosteidae										
Culaea inconstans	11	0.438	0.222	0.333	4.837	3	3	3	1	3
Ictaluridae										
Ameiurus melas	18	0.750	0.333	0.562	5.291	2	3	3	7	1
Ameiurus natalis	9	0.500	0.056	0.625	5.216	2	3	4	7	2
Ameiurus nebulosus	1	0.062	0.000	0.472	5.260	2	3	3	2	1
Ictalurus punctatus	10	0.250	0.333	0.394	6.257	2	3	4	8	2
Noturus flavus	22	0.562	0.722	0.816	6.057	3	1	1	2	3
Noturus gyrinus	8	0.375	0.111	0.634	4.825	5	3	3	8	2
Pylodictis olivaris	3	0.125	0.056	0.562	6.146	6	4	3	3	2
Hiodontidae										
Hiodon alosoides	1	0.000	0.056	0.355	4.138	3	4	3	3	2
Hiodon tergisus	3	0.125	0.100	0.367	4.170	3	4	...	3	3
Lepisosteidae										
Lepisosteus osseus	3	0.188	0.000	0.452	13.263	6	3	4	3	2
Lepisosteus platostomus	2	0.125	0.000	0.431	9.698	6	3	3	3	2
Percichthyidae										
Morone chrysops	6	0.188	0.167	0.355	3.491	6	3	1	3	2
Percidae										
Ammocrypta clara	2	0.062	0.056	0.440	8.857	5	2	2	3	...
Etheostoma aspirgene	1	0.062	0.000	0.615	5.415	5	3	4	2	...
Etheostoma caeruleum	9	0.188	0.333	0.607	4.512	5	1	1	4	3
Etheostoma exile	3	0.188	0.000	0.565	6.961	3	3	3	1	1
Etheostoma flabellare	17	0.438	0.556	0.628	5.351	5	2	1	1	2
Etheostoma nigrum	30	0.938	0.833	0.473	6.545	5	3	2	4	1
Etheostoma zonale	13	0.250	0.500	0.583	4.878	5	1	1	4	3
Perca flavescens	14	0.625	0.222	0.421	4.000	6	3	4	3	2
Percina caprodes	10	0.188	0.389	0.482	6.531	5	2	1	8	3
Percina evides	2	0.000	0.111	0.460	5.770	5	1	1	2	3
Percina maculata	23	0.625	0.722	0.500	6.814	4	2	1	7	2
Percina phoxocephala	11	0.250	0.389	0.482	6.032	5	1	1	2	3
Percina shumardi	1	0.062	0.000	0.538	6.098	5	1	1	3	...
Stizostedion canadense	8	0.250	0.222	0.348	6.618	6	3	4	3	2
Stizostedion vitreum	18	0.438	0.611	0.309	5.854	6	3	1	3	2
Petromyzontidae										
Icthyomyzon castaneus	5	0.062	0.222	0.857	13.143	8	3	...	6	...
Ichthyomyzon unicuspis	4	0.062	0.167	0.740	9.898	8	4	4	3	3
Lamptera appendix	3	0.062	0.111	0.684	12.590	1	2	1	2	3

APPENDIX 2. Continued.

Family Species name	Total sites	Variable sites	Stable sites	SwF	ShF	TR	WM	SUB	SS	TOL
Percopsidae										
Percopsis omiscomaycus	2	0.000	0.111	0.368	5.611	3	3	2	2	3
Salmonidae										
Coregonus hoyi	1	0.062	0.000	0.310	3.203	7	3	3	6	...
Oncorhynchus mykiss	9	0.250	0.278	0.370	5.146	6	2	1	4	3
Salmo trutta	13	0.375	0.389	0.372	4.382	6	2	1	4	3
Salvelinus fontinalis	4	0.125	0.111	0.382	4.585	6	2	4	1	3
Sciaenidae										
Aplodinotus grunniens	6	0.250	0.111	0.425	3.233	5	3	3	3	2
Umbridae										
Umbra limi	12	0.438	0.278	0.621	5.289	5	3	3	7	1

APPENDIX 3

Pearson correlation matrix for 25 functional attribute variables for 106 species grouped according to six major categories (see Table 1). R values with $P < 0.10$ using a Bonferroni correction are indicated by boldface and for $P < 0.05$, an "*" is used. HD = herbivore-detrivore, OM = omnivore, GI = general invertivore, SI = surface/water column invertivore, BI = benthic invertivore, PI = piscivore-invertivore, PL = planktivore, PA = parasite.

	Swim	Shape	HD	OM	GI	SI	BI	PI	PL	PA
Morphology										
Swim	1.000									
Shape	−0.278	1.000								
Trophic										
HD	0.109	0.045	1.000							
OM	−0.229	−0.357	−0.357	1.000						
GI	0.014	−0.569	0.000	0.466	1.000					
SI	**0.733***	−0.062	0.006	−0.412	−0.194	1.000				
BI	−0.079	0.454	0.187	**−0.612***	**−0.593**	0.048	1.000			
PI	−0.095	0.316	−0.334	−0.410	−0.523	0.072	−0.029	1.000		
PL	0.123	−0.176	−0.071	0.006	−0.040	−0.080	−0.258	0.243	1.000	
PA	−0.235	0.656	0.075	−0.486	**−0.631***	−0.065	0.389	0.480	−0.052	1.000
Current velocity										
Fast	0.090	0.269	0.221	−0.310	−0.118	0.112	0.576	−0.298	−0.270	−0.033
Moderate	−0.051	**0.599**	0.304	−0.423	−0.568	0.014	**0.587**	0.119	−0.187	0.418
Slow	0.103	−0.571	−0.285	0.392	0.418	0.061	**−0.679***	0.051	0.236	−0.248
General	−0.383	0.290	0.002	0.013	−0.058	−0.410	0.221	0.023	−0.008	0.020
Substrate										
Rubble	−0.074	0.570	0.305	−0.422	−0.411	−0.057	**0.686***	−0.067	−0.202	0.319
Sand	0.368	−0.107	0.379	0.134	0.454	0.229	−0.319	−0.454	−0.140	−0.318
Silt	−0.014	−0.439	−0.290	0.553	0.393	−0.109	−0.631	−0.059	0.198	−0.309
General	−0.037	−0.451	−0.384	0.053	0.049	0.092	−0.245	0.338	0.164	−0.130
Stream size										
Small	−0.380	−0.048	−0.361	**0.815***	0.304	−0.376	−0.321	−0.399	−0.292	−0.224
Md-Lg	0.235	0.168	0.130	**−0.691***	−0.369	0.317	0.659	0.155	−0.077	0.257
Sm-Lg	0.196	−0.210	0.332	−0.082	0.204	0.079	−0.455	0.184	0.384	−0.171
Lentic	−0.216	0.173	−0.301	0.108	−0.309	−0.210	−0.155	0.460	0.280	0.391
Tolerance										
High	0.002	**−0.604***	−0.272	**0.832***	**0.592**	−0.216	**−0.734***	−0.337	0.123	−0.560
Moderate	0.532	−0.139	0.239	−0.007	0.169	0.497	−0.370	−0.156	0.215	−0.133
Low	−0.286	0.354	−0.081	−0.506	−0.450	−0.150	**0.714***	0.302	−0.191	0.362

APPENDIX 3. Continued.

	Fast	Moderate	Slow	General	Rubble	Sand	Silt	General
Current velocity								
Fast	1.000							
Moderate	0.357	1.000						
Slow	**−0.726***	**−0.846***	1.000					
General	0.225	0.257	−0.549	1.000				
Substrate								
Rubble	**0.789***	**0.754***	**−0.941***	0.446	1.000			
Sand	−0.027	−0.088	0.128	−0.212	−0.173	1.000		
Silt	**−0.641***	**−0.741***	**0.839***	−0.348	**−0.861***	0.189	1.000	
General	−0.479	−0.360	0.494	−0.210	−0.541	−0.465	0.143	1.000
Stream size								
Small	−0.093	−0.254	0.167	0.104	−0.204	0.071	0.448	−0.190
Md-Lg	0.298	0.479	−0.432	0.027	0.441	−0.299	−0.607	0.149
Sm-Lg	−0.177	−0.317	0.316	−0.151	−0.276	0.384	0.199	−0.011
Lentic	−0.438	−0.074	0.249	−0.041	−0.282	−0.298	0.299	0.174
Tolerance								
High	−0.437	−0.560	**0.585**	−0.170	**−0.614***	0.236	**0.665***	0.187
Moderate	−0.290	−0.298	0.448	−0.467	−0.411	0.414	0.399	−0.039
Low	0.499	0.451	−0.627	0.447	0.660	−0.525	**−0.670***	−0.036

	Small	Md-Lg	Sm-Lg	Lentic	High	Moderate	Low
Stream size							
Small	1.000						
Md-Lg	**−0.664***	1.000					
Sm-Lg	−0.349	−0.448	1.000				
Lentic	0.151	−0.361	0.055	1.000			
Tolerance							
High	**0.590**	**−0.605***	0.095	0.025	1.000		
Moderate	−0.134	−0.171	0.412	−0.101	0.129	1.000	
Low	−0.307	0.564	−0.385	0.006	**−0.675***	**−0.765***	1.000