STREAMFLOW VARIABILITY, FISH COMMUNITY STRUCTURE, AND IMPLICATIONS FOR CLIMATIC CHANGE

by

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ABSTRACT

Relatively undisturbed U.S. streams were classified according to variation in 11 ecologically-relevant hydrologic characteristics. A group of 420 "best" stream sites and a group of 816 "acceptable" sites (including the 420 best sites) were evaluated with similar results. Cluster analysis resulted in the identification of 10 distinctly different stream types, seven perennial and three intermittent. Most of these stream types exhibit reasonable geographic affiliation and can be interpreted in terms of regional climatic patterns and local variation in geologic characteristics. The classification provides a comprehensive catalog for identifying streams that, according to ecological theory, may differ in major aspects of ecological organization. It further offers a basis for hypothesis-generation and affords an objective framework for matching streams for purposes of comparative ecological investigations. Moreover, the streamflow classification can be used to assess the *potential* ecological consequences of hydrologic changes, because specific kinds of hydrologic change induced by climatic changes (e.g., increased intermittency, reduced flood seasonality, etc.) can be compared to the historical hydrologic patterns summarized in this classification.

The sensitivity of measures of streamflow predictability and of high flow disturbance regime to variation in the time scale of analysis is investigated for the classified stream types. As the temporal scale was changed from daily to weekly to monthly to seasonal, six of the 12 stream types used in the analysis became more predictable, four less predictable, and two showed no change. For analysis of the high flow disturbance regimes across different stream types, monthly and annual data are not capable of capturing the information available in the daily hydrograph for most stream types. These results indicate the importance of regional climatic conditions and local catchment characteristics in influencing the calculation of predictability and high flow regimes at different time scales.

Stream fish assemblage data were analyzed for 34 sites in Wisconsin and Minnesota where long-term hydrologic data exist. Assemblages were analyzed in terms of both taxonomic and functional organization, and then related to independent hydrologic factors using multivariate statistical techniques. The taxonomic analysis showed strong geographic patterns among taxonomically-similar groups that reflected an interaction of species zoogeography and hydrologic regimes of surveyed streams. The functional analysis of the 34 assemblages revealed that two or three groups of sites could be defined in terms of functional organization (i.e., body morphology, trophic guild, habitat preferences, and tolerance values). These functionally-similar groups were strongly correlated with independent hydrologic factors that differed significantly among the 34 sites. Fish assemblages defined in functional terms could be assigned to hydrologically variable, stable, and very stable sites. These hydrologic-community relations suggest that climatic change which alters hydrologic regimes in this region can modify stream fish assemblage structure. Community changes are more likely to be detected using a functional rather than a purely taxonomic perspective.

ACKNOWLEDGMENTS

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SECTION 1

A STREAMFLOW CLASSIFICATION OF U.S. STREAMS AND RIVERS, AND ITS USEFULNESS FOR CLIMATE CHANGE RESEARCH

INTRODUCTION

Streamflow is arguably the most characteristic physical attribute of stream ecosystems, and it plays a central role in stream ecology (see Hynes 1970). Because many important structural attributes in streams, such as habitat volume, current velocity, channel geomorphology and substrate stability, are under the direct influence of streamflow, measurement of streamflow can represent an integration of complex environmental conditions that are individually difficult to quantify.

Global climate change is expected to alter large-scale patterns of precipitation, which will in turn affect lotic ecosystems by modifying streamflow regimes (Poff 1992). To the extent that species distributions and abundances reflect physical streamflow patterns, climate-induced changes could potentially affect lotic ecosystems throughout the entire United States. It is thus imperative that the existing relationships between physical characteristics of lotic ecosystems and ecological patterns be established in order to provide a baseline frame of reference for future interpretation of impacts attributed to climate change. A necessary first step in this process is the identification of currently existing hydrological characteristics that constrain the distributions and abundances of species at regional scales. This requires that hydrologic data be expressed explicitly in terms of environmental selective forces for lotic biota.

In streams, flow fluctuations and extreme conditions such as floods and low flow are primary sources of environmental variability and disturbance (cf. Stanford and Ward 1983). Patterns of diversity of all major lotic assemblages, including fish (Seegrist and Gard 1972, Harrell 1978, Horwitz 1978, Minckley and Meffe 1987), invertebrates (Vannote et al. 1980, Ward and Stanford 1983, Bournard et al. 1987), attached algae (Patrick 1975, Peterson 1987, Power and Stewart 1987) and macrophytes (Haslam 1978, Ladle and Bass

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1981) have been related to patterns of temporal variation in flow. Moreover, there is a substantial body of evidence indicating that both high flow (flood) and low flow (intermittency) disturbances play a central role in structuring stream communities (Hynes 1970, Williams and Hynes 1976, 1977, Iversen et al. 1978, Fisher 1983, Stanford and Ward 1983, Ward and Stanford 1983, Schlosser 1987, Delucchi 1988, Minshall 1988, Power et al. 1988, Resh et al. 1988).

Geographic variation in streamflow patterns can be evaluated in many ways, but one of the most useful is classification, where similar "types" of hydrologic regimes are identified and associated. The scale at which streamflow classifications have been previously constructed range from regional (Gentilli 1952, Dewberry 1980, Alexander 1985, Hughes and James 1989, Jowett and Duncan 1990, Richards 1990) to continental (Grimm 1968, Poff and Ward 1989) to global (Beckinsale 1969, McMahon 1979, 1982, Haines et al. 1988).

Different combinations of streamflow variation (e.g., range and predictability), patterns of flooding (e.g., frequency and predictability) and extent of intermittency presumably result in different degrees of physical control over biotic organization (Minshall 1988, Resh et al. 1988, Poff and Ward 1989, 1990). Most comparative geographical studies have considered only a few measures of flow variability, e.g., mean flow conditions (Hawkes et al. 1986, Moss et al. 1987, Townsend et al. 1987), variation about the mean flow (Horwitz 1978), short-term estimates of flood frequency (Cushing et al. 1980, 1983, Minckley and Meffe 1987, Fisher and Grimm 1988), and predictability of monthly flow patterns (Resh et al. 1988, Bunn et al. 1986). Fewer comparative studies have considered several hydrologic factors simultaneously (Poff and Ward 1989, Hughes and James 1989, Jowett and Duncan 1990).

There are several reasons to classify streamflow regimes with an eye toward the potential impacts of climate change. First, it is necessary to establish historical (background) patterns in hydrologic regimes to establish a baseline against which future changes must be measured. The importance of establishing baseline hydrologic patterns prior to potential climate change from a general water resources perspective has been recently emphasized (Wallis et al. 1991, Dolph and Marks 1992). Second, spatial distribution of hydrologic regimes may help us to develop testable hypotheses about environmental constraints on regional processes and patterns in lotic systems (cf. Resh et al. 1988, Poff and Ward 1989, Minshall 1988). Placing stream

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ecology into a regional context is needed to consider potential impacts of climate change (Poff 1992, Grimm 1992, Carpenter et al. 1992). Third, a hydrogeographic classification can help to identify specific regions that are especially sensitive to potential alterations in amount and/or timing of precipitation brought on by climate change. Thus, we may infer something useful about what specific types of changes may be most important ecologically in different regions, which differ in *historical* (i.e., pre-climate change) hydrology. For example, desert streams are very sensitive to increased aridity (Dahm and Molles 1992, Grimm and Fisher 1992) while more baseflow-driven systems may be buffered against aridity but are potentially sensitive to increased flow variability (Poff 1992). We need to know the geography of such ecological sensitivities, because potentially valuable resource management information can be revealed, as has been demonstrated when this approach is applied to questions of water resource distribution (Gleick 1990).

The objective of this research was to provide a large-scale framework to allow classification of naturally-flowing streams and rivers on the basis of ecologically-important hydrologic characteristics. An earlier analysis (Poff and Ward 1989) used 78 streams to show that extensive hydrologic variation of ecological interest exists for U.S. streams and rivers. This paper reports on an extension of that earlier effort and it serves two major purposes. First, the characterization of hydrologic similarity among all gauged, free-flowing streams in the U.S. allows individuals/agencies interested in examining hydrological-ecological relationships to identify sites that share ecologically-important hydrologic regimes. Proper site-matching is a necessary condition in any cross-community comparisons in streams (Resh et al. 1988, Fisher and Grimm 1991). Second, by examining *all* candidate streamflow data available for the entire continental U.S., the paper provides a *comprehensive* classification that characterizes "pre climate change" hydrologic regimes at a continental scale.

METHODS

Site Selection

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. For each of the ca. 7000

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stations in the dataset, the "Remarks" section was read to determine if the stream met certain specific criteria: (1) minimal or no flow regulation (e.g., diversion, damming, groundwater pumping), (2) minimal or no watershed urbanization, (3) ≥ 20 yr of continuous daily streamflow data, preferably extending up through water year 1985, and (4) an accuracy rating of "good" or better for the recorded flow values in the water years chosen. However, the occurrence of a few days with "poor" or "fair" records (due to, for example, ice blockage) was not sufficient reason alone to exclude the station. This process generated ca. 2200 sites that *potentially* could be used for the streamflow classification. Of these 2200 sites, ca. 1000 were of unknown quality because there was no available description available for them in the "Remarks" section of the Earth-Info database (usually because the gauge was discontinued). This exhaustive list of potential sites was then compared with two independently-derived datasets. First, Slack and Landwehr (1992) identified 1659 stream gauging sites in the U.S. and its territories having at least 20 yr of record extending through 1988 during which no "confounding anthropogenic influences" occurred. These sites were identified based on information collected from state water resource experts in the district offices of the USGS, and they therefore represent a very reliable dataset characterizing gauging station quality. However, not all sites identified by Slack and Landwehr (1992) could be used for the streamflow classification, because their criteria allowed inclusion of sites having only monthly flow data and sites having significant flow impairment over the entire period of record (POR). For example, a regulated river with highly modified flow regime could be included in their dataset if the extent of flow regulation had not changed significantly over the POR. A second dataset identifying reliable, long-term stream gauging stations with unimpaired flow was put together by Wallis et al. (1991). They selected sites based on readings of the "Remarks" section in the Earth-Info database. They identified 1014 unregulated or minimally regulated sites with daily flow records extending from 1948-1988. Some of the sites used by Wallis et al. (1991) had gaps in the record, and they estimated missing values with regression analysis, using data from nearby gauges.

Comparison of the original 2200 sites with the two independent datasets resulted in 812 sites matching the Slack and Landwehr (1992) dataset and an additional 90 matching with the Wallis et al. (1991) dataset. Only sites

having catchment area $\leq$ 5000 km^2 and estimated average flood durations < 15 d were retained in the final dataset, which consisted ultimately of 733 sites from Slack and Landwehr (1992) and 83 sites from Wallis et al. (1991). This final dataset (N = 816) was partitioned into two subsets: one containing 420 sites with POR ending in 1985 and at least 36 yr in length, and a second containing all 816 matched sites having at least 20 yr of continuous daily flow data with the last year in the record not occurring before 1978. These two subsets were analyzed separately to provide 1) a core classification of the "best" gauged sites available (N = 420) in the U.S., and 2) a classification of all "acceptable" sites (N = 816), which, while satisfying less rigorous criteria, nonetheless represents the exhaustive classification based on available data. The names and locations of these sites are provided in Appendix A (data file on diskette).

Definition of Flow Variables

Several variables were defined for extraction from the long-term hydrologic records. A computer program written in True-Basic language (Appendix B, also included on diskette) to extract hydrologic variables. They fell into four general categories (listed as I-IV below). The periods of record for different streams varied in length, and this may have caused subtle differences to arise in the values of derived statistics that were used in the classification process. In order to account for this bias in length of available record, many of these variables were also derived for a 20-yr period as well as for the entire period of record. For sites exceeding 20 yr in length of record, the period 1966-1985 was selected where possible so that all sites shared the same short period. For sites with records terminating prior to 1985, the most recent 20 yr period was selected, except for sites with records terminating prior to 1978, when no short record was analyzed. The values of the extracted variables for each site are included in Appendix C (also on diskette).

Basin Descriptors--

These are static measures indicative of stream/catchment size. These variables are readily available from the "Remarks" section of the Earth-Info CD-ROM database (an electronic facsimile to the gauging station summaries in

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the Water Supply papers published annually by the USGS) and contain no information about hydrologic variability.

Basin Drainage Area (AREA, km^2)--The surface area of the catchment topographically above the gauge elevation.

Daily Mean Discharge (QMEAN, m^3 sec^{-1})--The average daily flow at the site over all years in the record.

Mean Annual Runoff (MAR, mm yr^{-1})--Ratio of QMEAN/AREA expressed as a depth. MAR represents the difference between annual evaporation and precipitation (Gordon et al. 1992). This index was suggested by Hughes and Omernik (1983) as a substitute for stream order in classifying stream and catchment size across different hydroclimatological regions.

In order to allow unbiased comparisons of hydrologic variability among streams that vary greatly in catchment size and annual runoff, it was necessary to "modularize" the data (Yevjevich 1972) by dividing each daily flow value by QMEAN for the entire POR. Thus, for each stream, the modularized mean flow was 1.0.

Measures of Flow Variability and Predictability--

These measures assess the degree of variation in the hydrologic signal with no special treatment of extreme flow values.

Baseflow Index (BFI, %)--For each year in the POR, the ratio of the lowest daily flow to the average daily flow indexes flow stability and susceptibility to drying. The average of all the annual ratios was calculated as the BFI and multiplied times 100.

Coefficient of Variation (DAYCV, %)--This dimensionless index represents the average (across all years) of the ratios between the annual mean daily flow and the standard deviation of the daily flows, multiplied by 100 and expressed as a percent. DAYCV describes overall flow variability without considering the temporal sequence of flow variation.

Predictability of Flow (DAYPRED, %)--DAYPRED was determined using an index developed by Colwell (1974) which is based on information theory. When expressed as a percent, this index ranges in value from 0 to 100 and is composed of two independent, additive compoenents: constancy (C), a measure of temporal invariance, and contingency (M), a measure of periodicity. The index can be used to express the degree to which flow "states" (i.e., quantity of discharge) are predictably distributed across specified time intervals.

Predictability values are sensitive to definition of flow states, which are ultimately arbitrary (Gordon et al. 1992). In this analysis, 11 categories were defined with 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 modularized mean flow. Thus, the 11 flow states ranged from < 12.5% of mean flow to >640% of mean flow. Predictability measures are also sensitive to length of record. Gan et al. (1991) used monthly flow data to show that short POR tend to yield overestimates of predictability, whereas records in excess of ca. 40 yr yielded stable estimates of predictability. Gordon et al. (1992) point out that more comparative studies are needed to develop consistent methodologies in the application of Colwell's index to ecologically-relevant hydrologic variability (see Section 2 this report.)

High Flow Disturbance--

This was defined as flows of magnitude exceeding the theoretically-expected return interval of 1.67-yr based on a log-normal distribution. The "annual peak flow series" for each station was used to determine these flood values, because the peak series provides the maximum *instantaneous* (rather than 24-hr) flow values that are needed to properly determine flood frequencies. The peak values were assumed to represent a sample from a log-normal distribution (see Dunne and Leopold 1978, p. 306); hence, by knowing the mean and variance of the sample, one can calculate floods of specified probability of occurrence (e.g., a 2-yr flood has a 50% probability of occurring in any given year and is represented by the mean value of the annual series on a logarithmic scale). A flow with a 1.67-yr return interval is often recognized as "bankfull," but this may vary regionally and with climate. The bankfull stage, according to Dunne and Leopold (1978, p. 608) corresponds to the "discharge at which channel maintenance is most effective . . . in doing work that results in the average morphologic characteristics of the channels." Thus, this level of flow can be considered a non-arbitrary index of physical habitat disturbance in streams (see Poff and Ward 1989).

Flood flows exceeding the return intervals of 1.67 yr were determined to encompass the range of potential bankfull discharge across many stream types. (Ideally, geomorphic information is needed to determine the most appropriate level of flow to be selected as the proper site-specific index of flood disturbance.) After determining these threshold flow levels, the flood history

for a site was determined by regressing the log of the peak flow values against the log of the corresponding 24-hr mean flows (i.e., those occurring on the same dates as the peak flows) so that "daily flood" values could be determined. The long-term daily flow record was then analyzed with respect to these "daily flood" values. Several measures were derived for the entire period of record.

Inter-annual Variability (FLODVAR, dimensionless)--The standard deviation of the annual peak flow series on a log scale is a measure of between-year variation in flood magnitude. This statistic was called the Flash Flood Frequency Index by Beard (1975, see also Baker 1977, 1988), and it can be used to assess stability in maximum annual flows.

Frequency (FLODFREQ, yr^{-1})--The average number of discrete flood events per year having a magnitude equalling or exceeding that associated with the 1.67 yr return-interval flood. The number of days that separate independent flood events may vary geographically; therefore, a 10-d period separating individual bankfull events was used as a criterion to identify separate spates.

Duration (FLODDUR, d)--The average number of days that flow remains above the flood threshold for a site.

Seasonal Predictability of Flooding (FLDPRED, dimensionless)--Maximum proportion of all floods over the period of record that fall in any 60-d "seasonal window." This index ranges from 0.167 ("random" flooding) to 1.0 (perfectly seasonally predictable) For this metric, the "partial duration series" from the Earth-Info CD-ROM was used. All instantaneous flows $\geq$ 1.67 yr return-interval flow in the period of record were ordered according to on which day of the year they occurred and the temporal distribution of this collapsed data set was analyzed for seasonal patterns. High flows occurring within 60 days of the beginning or end of the water year were considered to fall within the same "season".

In addition, the day of the water year marking the beginning of the 60-d period when FLDPRED was highest was recorded by the variable FLDTIME. This variable was not used as a primary classification variable, but was used to evaluate the range of timing of flood-onset within groups of hydrologically-similar streams as identified by the cluster analysis.

Seasonal Predictability of Non-flooding (FLDFREE, dimensionless)-- Maximum proportion of year (#days/365) during which no floods have ever

occurred over period of record. Again, the partial series was used and no-flood periods were allowed to pass through the end of one water year into the beginning of the next.

Low Flow Disturbance--

Low flows were characterized both by identifying periods of zero discharge and by calculating site-specific lowflows of specified return intervals. The latter was accomplished by taking the annual 1-day minimum 24-hr low flow values for a station and assuming that they represent a sample from a population with a Gumbel (extreme value) distribution (Linsley et al. 1982, p. 375). The parameters from this distribution were used to calculate one-day low flows with various return intervals. The long-term daily record was scanned to locate periods when low flows with $\geq$ 5-yr recurrence intervals occurred. Several variables were derived from this analysis.

Extent of Intermittency (ZERODAY, d)--Average annual number of days having zero discharge.

Seasonal Predictability of Lowflow (LOWPRED, dimensionless)--Proportion of low flow events $\geq$ 5-yr magnitude falling in a 60-d "seasonal window" (as described above for flood predictability). Also, the variable LOWTIME was derived to evaluate within-cluster variation in timing of lowflow-onset.

Seasonal Predictability of Non-lowflow (LOWFREE, dimensionless)--Maximum proportion of year (#days/365) during which no 5-yr+ low flows have ever occurred over period of record.

Statistics

Basic relationships among hydrologic variables--

Pearson correlation coefficients were derived for linear relations among all 14 variable combinations. For the 11 hydrologic variables, the correlation matrix was used as input into a principal components analysis (PCA), a multivariate technique for examining relationships among several quantitative variables. The goal of PCA is to derive a small number of linear combinations of the original variables that retain the maximum possible amount of information in the original variables (SAS 1988). This procedure represents a dimensional reduction of many variables to a few principal

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components, the interpretation of which is often facilitated by a further transformation known as "rotation" (SAS 1988).

Streamflow Classification--

Several criteria were used to identify meaningful classifications of the stream sites. First, three categories were defined based on a priori ecological considerations: (1) "permanent" streams (ZERODAY < 10 days per year); (2) "intermittent" streams (ZERODAY between 10 and 90 days, inclusive); (3) "harsh" streams (ZERODAY > 90 days per year). These divisions, while arbitrary, reflect the established ecological importance of flow permanence in regulating lotic process and pattern (e.g., Grimm 1992, Ward 1992, Delucchi 1988, 1989, Valett and Stanley 1992)

The "permanent" group was a heterogeneous set of 383 data points, representing streams with reasonably stable characteristics. To further characterize these streams we applied a cluster analysis using the two-stage density linkage method provided in SAS's PROC CLUSTER. This is a non-parametric clustering, utilizing a k-th nearest neighbor criterion, which seeks regions surrounding local maxima in the estimated probability density function associated with a set of variables. Simulations suggest that the method does reasonably well when the true clusters are known to be of unequal size and variability, or when the clusters are irregularly (e.g. nonconvex) shaped (SAS 1988). Since we had no a priori expectations regarding the shape, size, or dispersion of stream clusters, we felt that such a non-parametric approach was reasonable. The two-stage density linkage method was also applied separately to the intermittent and harsh streams.

Determining the number of clusters in an arbitrary data set is a problem which lacks a clear statistical solution. Following the idea of Wong and Schaack (1982), we applied the clustering algorithm with different values for the nearest neighbor parameter. We looked for clustering solutions which gave fairly consistent estimates of the number of modes of the distribution across a range of parameter values, while at the same time yielding clusters with clear interpretations. In this admittedly subjective process, we gave precedence to scientific interpretability rather than to arbitrary criteria based on unsupportable statistical assumptions. A distinct advantage of this method versus other k-th nearest neighbor methods (e.g., K-means clustering used by Poff and Ward 1989) is that individual sites are always assigned to

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the same cluster for a fixed sample size. K-means clustering produces slightly different cluster memberships depending on the initial input order of the sites.

Stream cluster stability--

Given that the number of clusters was arbitrarily set, it is critical that the stability of the putative clusters be examined. In order to avoid reliance on parametric assumptions, a method based on bootstrapping, a computer-intensive method of drawing repeated resamples from the original data (Efron 1979), was developed by Dr. Daniel Denman (Department of Statistics, University of Maryland). First, 383 resamples were drawn with replacement (i.e., the same stream could be drawn more than once) from the original set of 383 points in the "permanent" stream dataset. Second, the two-stage density linkage clustering algorithm was applied to identify 7 clusters from the "new" collection of 383 points. Third, the set of resampled points was assessed in terms of the number of points sharing membership both in a resample-derived cluster as well as in an original cluster. Two indices were computed for the resample. $M_{o|r}$ is the proportion of points in resample clusters which also were together in original clusters, and it represents the extent to which resample clusters represent the membership structure of the original clusters. $M_{r|o}$ is the proportion of points in original clusters which also were together in resample clusters, and it represents the tendency for points originally clustered together to stay together, regardless of to which resample cluster they are assigned. Fourth, this process was repeated until the average values of $M_{r|o}$ and $M_{o|r}$ stabilized (N=200).

RESULTS

The geographical locations of the 420- and 816-site samples are shown for the 48 conterminous states in Figure 1. Gauged stream sites were available from all states and for most ecoregions and USGS hydrologic units. The gauged sites exhibited a wide range of values for several important static descriptors, including catchment area (Figure 2), mean daily flow (Figure 3), mean annual runoff (Figure 4), gauge elevation (Figure 5), and period of record (Figure 6).

TABLE 1. MATRIX OF PEARSON CORRELATION COEFFICIENTS FOR 14 VARIABLES ON 420 STREAMS. VARIABLE DEFINITIONS ARE GIVEN IN METHODS. SIGNIFICANT CORRELATIONS (BONFERRONI TEST) ARE: R > 0.12, P < 0.05; R > 0.13, P < 0.01; P > 0.15, P < 0.001.

	AREA	QMEAN	MAR	DAYCV	DAYPRED	BFI	ZERODAY	FLDFREQ	FLDPRED	FLDFREE	FLDDUR	FLDVAR	LOWPRED	LOWFREE
AREA	1.00													
QMEAN	0.57	1.00												
MAR	-0.23	0.41	1.00											
DAYCV	-0.03	-0.27	-0.34	1.00										
DAYPRED	0.10	0.44	0.42	-0.73	1.00									
BFI	-0.01	0.07	0.09	-0.56	0.60	1.00								
ZERODAY	-0.07	-0.16	-0.18	0.60	-0.23	-0.19	1.00							
FLDFREQ	0.15	-0.08	-0.23	0.39	-0.32	-0.12	0.34	1.00						
FLDPRED	0.09	0.16	0.09	-0.12	0.28	0.06	0.03	-0.14	1.00					
FLDFREE	0.07	0.15	0.15	-0.02	0.20	0.03	0.09	-0.04	0.81	1.00				
FLDDUR	0.25	0.02	-0.24	-0.12	0.07	0.07	0.10	0.13	0.59	0.55	1.00			
FLDVAR	-0.07	-0.16	-0.19	0.26	-0.23	-0.10	0.11	0.22	-0.24	-0.13	0.12	1.00		
LOWPRED	-0.19	0.16	0.38	-0.23	0.25	-0.26	-0.20	-0.31	-0.03	-0.01	-0.19	-0.07	1.00	
LOWFREE	-0.18	0.20	0.39	-0.32	0.28	-0.28	-0.28	-0.31	-0.04	-0.04	-0.19	-0.06	0.85	1.00

TABLE 3. MATRIX OF PEARSON CORRELATION COEFFICIENTS FOR 14 VARIABLES ON 816 STREAMS. VARIABLE DEFINITIONS ARE GIVEN IN METHODS. SIGNIFICANT CORRELATIONS (BONFERRONI TEST) ARE: R > 0.12, P < 0.05; R > 0.13, P < 0.01; P > 0.15, P < 0.001.

	AREA	QMEAN	MAR	DAYCV	DAYPRED	BFI	ZERODAY	FLDFREQ	FLDPRED	FLDFREE	FLDDUR	FLDVAR	LOWPRED	LOWFREE
AREA	1.00													
QMEAN	0.57	1.00												
MAR	-0.23	0.36	1.00											
DAYCV	-0.01	-0.27	-0.36	1.00										
DAYPRED	0.09	0.41	0.40	-0.57	1.00									
BFI	0.02	0.09	0.09	-0.52	0.58	1.00								
ZERODAY	-0.02	-0.18	-0.24	0.67	-0.13	-0.24	1.00							
FLDFREQ	0.09	-0.08	-0.22	0.25	-0.29	-0.12	0.21	1.00						
FLDPRED	0.07	0.12	0.08	-0.11	0.31	0.04	0.04	-0.15	1.00					
FLDFREE	0.05	0.09	0.14	-0.04	0.26	0.02	0.09	-0.09	0.82	1.00				
FLDDUR	0.26	0.02	-0.24	-0.07	0.13	0.04	0.17	0.08	0.61	0.56	1.00			
FLDVAR	-0.00	-0.15	-0.22	0.28	-0.22	-0.10	0.20	0.22	0.01	0.04	0.13	1.00		
LOWPRED	-0.20	0.14	0.38	-0.31	0.22	-0.16	-0.30	-0.24	0.02	0.03	-0.17	-0.12	1.00	
LOWFREE	-0.23	0.15	0.42	-0.39	0.28	-0.13	-0.38	-0.23	0.01	0.02	-0.18	-0.13	0.84	1.00

<u>Statistical Correlations among Variables</u>

The statistical relationships between the hydrological variables were explored with correlation analysis and principal components analysis (PCA). Table 1 shows that for the 420-site sample, many variables were significantly correlated, despite the low correlation coefficients, because sample size was very large. For the 11 primary classification variables, the correlation matrix was used as input into a principal components analysis (PCA) to determine how much of the total variance in the variable data space could be explained by dimensional reduction. Table 2 shows that 4 principal component axes explained 76% of the total variation among the 420 sites. The first axis essentially represents a contrast between flow stability (high predictability and baseflow) and variability (high negative coefficient of variation and intermittency). The second axis emphasizes flood predictability and duration, while the third reflects low flow predictability. The fourth axis describes variation due to inter-annual flood intensity. Interestingly, the flood frequency variable does not have a high loading on any factor, which suggests that among-site variation in this variable is small relative to the other variables.

TABLE 2. MATRIX OF ROTATED (VARIMAX) PCA FACTOR LOADINGS
THE 11 VARIABLES USED IN THE ANALYSIS OF 420 STREAMS. BOLDFACE
NUMBERS INDICATE VARIABLES WITH HIGHEST FACTOR LOADINGS

	FACTOR1	FACTOR2	FACTOR3	FACTOR4
DAYCV	**-0.902**	-0.062	-0.197	-0.132
DAYPRED	**0.775**	0.236	0.151	0.223
BFI	**0.794**	0.024	-0.430	0.044
ZERODAY	**-0.615**	0.157	-0.294	0.059
FLDFRQ	-0.363	-0.041	-0.407	-0.402
FLDPRED	0.079	**0.923**	0.032	0.073
FLDFREE	-0.018	**0.910**	0.029	0.032
FLDDUR	0.053	**0.771**	-0.185	-0.190
FLDVAR	-0.109	0.075	0.007	**-0.931**
LOWPRED	0.066	-0.038	**0.923**	0.047
LOWFREE	0.145	-0.065	**0.924**	0.012
Variance explained	2.60	2.37	2.24	1.153
Cumulative proportion	0.24	0.44	0.65	0.76

TABLE 4. MATRIX OF ROTATED (VARIMAX) PCA FACTOR LOADINGS
THE 11 VARIABLES USED IN THE ANALYSIS OF 816 STREAMS. BOLDFACE
NUMBERS INDICATE VARIABLES WITH HIGHEST FACTOR LOADINGS

	FACTOR1	FACTOR2	FACTOR3	FACTOR4	FACTOR5
DAYCV	-0.540	-0.073	-0.237	-0.134	**-0.719**
DAYPRED	**0.838**	0.226	0.244	0.196	0.037
BFI	**0.867**	-0.035	-0.260	0.002	0.249
ZERODAY	-0.084	0.092	-0.228	-0.104	**-0.884**
FLDFRQ	-0.281	-0.043	-0.299	**-0.647**	0.110
FLDPRED	0.089	**0.923**	0.053	0.097	-0.015
FLDFREE	0.053	**0.901**	0.072	0.048	-0.077
FLDDUR	0.040	**0.805**	-0.194	-0.171	0.026
FLDVAR	0.017	0.050	0.064	**-0.842**	-0.283
LOWPRED	-0.010	-0.025	**0.926**	0.079	0.138
LOWFREE	0.036	-0.032	**0.918**	0.070	0.227
Variance explained	1.85	2.34	2.07	1.25	1.53
Cumulative proportion	0.17	0.38	0.57	0.68	0.82

Similar patterns emerged for the 816-site sample. Significant correlations among hydrologic variables (Table 3) were frequent, despite low correlation coefficients. The correlation structure was very similar to that for the 420-site sample, indicating that variable periods of record did not seriously influence the underlying relationships among hydrologic variables. Five factors were required to explain 82% of the total among-site variation. The PCA for the 816-site sample was similar to the 420-site sample, except that the importance of flow variability (coefficient of variation and intermittency) was transferred from the 1st to the 5th axis, and flood frequency had a relatively high weight on the 4th axis (Table 4).

Cluster Results: Statistical Relationships

For the 420- and 816-site samples, 10 clusters were formed into groups of "permanent" and "intermittent" streams, which were given 2-letter or 3-character alpha-numeric abbreviations (Table 5). Among the intermittent streams, sites having > 90 days of zero flow per year were characterized as "Harsh Intermittent" (HI). Streams with less continuous intermittent conditions (10 < ZERODAY ≤ 90) fell into two clusters: "Intermittent Flashy"

TABLE 5. LISTING OF ABBREVIATIONS FOR 10 CLUSTERS
FORMED IN THE 420- AND 816-SITE SAMPLES.

Category	Abbreviation		Description
Perennial			
	PR		Perennial Runoff
	GW		Stable Groundwater
	SS		Supterstable Groundwater
	SR		Snow + Rain
		SR1[*]	Snow + Rain, type 1
		SR2[*]	Snow + Rain, type 2
	SN		Snowmelt
		SN1[**]	Snowmelt, type 1
		SN2[**]	Snowmelt, type 2
	PF		Perennial Flashy
Intermittent			
	IR		Intermittent Runoff
	IF		Intermittent Flashy
	HI		Harsh Intermittent

[*] Clusters formed only for N = 420 sites
[**] Clusters formed only for N = 816 sites

(IF) and "Intermittent Runoff" (IR) streams. The permanent groups of streams had less than 10 days of zero flow per year on average. For this group, solutions with 4 to 9 clusters were considered and compared in terms of interpretability and repeatability. A 7-cluster solution was accepted as optimal for the permanent streams. For the 420- and 816-site samples, 6 clusters were shared: "Perennial Runoff" (PR), "Stable Groundwater" (GW), "Superstable Groundwater" (SS), "Snow+Rain" (SR), "Snowmelt" (SN), and "Perennial Flashy" (PF) streams. For the 420-site sample, the 7th cluster was a variant of "Snow+Rain" (SR2), while for the 816-site sample, the 7th cluster was a variant of "Snowmelt" (SN2).

The statistical properties of these 10 clusters (7 permanent + 3 intermittent) are given for the 420-site sample in Table 6, which indicates sources of significant variation among clusters in terms of the ecologically-important hydrologic variables. For the intermittent streams, the Harsh Intermittent (HI) group averages 190 days per year without flow. The Intermittent Flashy (IF) and Intermittent Runoff (IR) groups show many fewer

TABLE 6. NUMERICAL MEANS AND STANDARD DEVIATIONS (IN PARENTHESES) OF 11 VARIABLES FOR 10 CLUSTERS FOR 420 GAUGED STREAM SITES. VARIABLES INDICATED BY "*" WERE NOT INCLUDED IN THE TWO-STAGE CLUSTER ROUTINE AT ANY TIME, BUT ARE INCLUDED FOR COMPARATIVE PURPOSES. FOR INTERMITTENT STREAMS, EXCLUDED VARIABLES ARE INDICATED BY "--"

	Perennial Runoff (PR)	Mesic Groundwater (GW)	Super Stable (SS)	Snow + Rain (SR1)	Snow + Rain (SR2)	Snowmelt (SN)	Peren. Flashy (PF)	Intermit. Runoff (IR)	Intermit. Flashy (IF)	Harsh Intermit. (HI)
N	209	55	17	27	29	22	24	20	10	7
DAYCV	173.5 (46.9)	114.3 (36.9)	86.4 (49.1)	167.4 (40.5)	111.6 (28.8)	134.1 (27.3)	270.4 (42.1)	289.2 (91.0)	474.5 (85.3)	481.0 (123.0)
DAYPRED	56.0 (11.6)	72.7 (3.9)	73.2 (5.5)	64.9 (9.3)	76.0 (7.0)	78.8 (10.5)	34.0 (9.8)	29.8 (7.2)	20.4 (4.7)	47.1 (13.6)
BFI	7.3 (5.6)	27.8 (8.1)	47.5 (16.8)	5.4 (3.9)	18.2 (8.3)	15.8 (8.5)	4.4 (6.4)	--	--	--
ZERODAY	0.4 (1.3)	0 (0)	0 (0)	0.4 (1.7)	0.02 (0.12)	0.05 (0.02)	2.4 (2.9)	21.7 (8.5)	43.7 (17.4)	189.7 (58.7)
FLDFREQ	0.69 (0.13)	0.80 (0.16)	0.66 (0.09)	0.75 (0.16)	0.68 (0.08)	0.65 (0.10)	0.97 (0.13)	0.79 (0.16)	0.94 (0.19)	1.04 (0.30)
FLDVAR	0.32 (0.21)	0.31 (0.10)	0.27 (0.14)	0.37 (0.23)	0.26 (0.11)	0.25 (0.18)	0.37 (0.17)	0.43 (0.30)	0.40 (0.13)	0.44 (0.32)
FLDPRED	0.47 (0.12)	0.43 (0.09)	0.62 (0.14)	0.68 (0.11)	0.68 (0.14)	0.97 (0.06)	0.48 (0.11)	0.55 (0.15)	0.46 (0.13)	0.58 (0.14)
FLDFREE	0.23 (0.12)	0.19 (0.11)	0.37 (0.14)	0.57 (0.09)	0.46 (0.10)	0.79 (0.11)	0.31 (0.13)	0.39 (0.20)	0.19 (0.12)	0.46 (0.16)
FLDDUR	3.0 (2.5)	2.6 (1.6)	4.3 (2.4)	2.9 (1.6)	3.7 (2.5)	9.6 (2.7)	2.8 (0.9)	--	--	--
LOWPRED	0.74 (0.16)	0.61 (0.14)	0.43 (0.07)	0.87 (0.10)	0.78 (0.16)	0.70 (0.17)	0.48 (0.11)	0.61 (0.13)	0.46 (0.05)	0.49 (0.16)
LOWFREE	0.64 (0.17)	0.51 (0.17)	0.26 (0.09)	0.76 (0.10)	0.66 (0.18)	0.62 (0.16)	0.31 (0.13)	0.53 (0.20)	0.16 (0.05)	0.25 (0.17)
AREA*	1128 (1068)	1324 (1155)	1144 (1100)	546 (518)	1099 (983)	1417 (1322)	1310 (890)	1133 (986)	845 (573)	644 (524)
QMEAN*	13.0 (12.8)	17.5 (14.7)	11.5 (8.8)	20.2 (24.3)	27.6 (27.8)	23.7 (30.5)	8.4 (5.9)	5.2 (5.0)	3.0 (2.4)	0.4 (0.2)
MAR*	0.44 (0.26)	0.49 (0.21)	0.44 (0.40)	1.28 (0.94)	1.11 (0.96)	0.43 (0.20)	0.22 (0.12)	0.22 (0.18)	0.12 (0.02)	0.03 (0.03)
POR*	49.7 (7.0)	50.4 (6.5)	50.4 (5.8)	46.1 (7.8)	49.2 (7.2)	49.1 (7.0)	47.0 (7.3)	43.9 (7.1)	43.8 (5.7)	43.0 (6.9)

days of no discharge while differing from one another both in terms of average intermittency and average flood frequency. Among the permanent streams, the Snowmelt (SN) group sites have very high seasonality of flooding, the Snow+Rain streams (SR) have intermediate seasonality of flooding coupled with very high seasonality of lowflow and either a stable (SR2) or variable (SR1) daily flow. The Perennial Runoff streams (PR) are characterized by low flood seasonality coupled with high seasonality of lowflow and variable daily flow. The Stable Groundwater (GW) group has low variability in daily flow coupled with aseasonal flooding, while the Superstable (SS) streams express extremely stable daily flow. The Perennial Flashy (PF) group exhibits high flow variability and high flood frequency with low seasonality for both floods and lowflow events.

The clusters for the 816-site sample are segregated in very similar fashion (Table 7) except that two snowmelt groups (rather than two snow+rain groups) were formed. The main statistical distinction between these two groups in terms of the hydrologic variables was that one group had greater daily flow stability and higher seasonal predictability of lowflow conditions.

Graphical comparison of clusters in terms of hydrologic variables reveals striking or subtle differences for DAYCV (Figure 7), DAYPRED (Figure 8), FLDFRQ (Figure 9), FLDPRED (Figure 10), FLDFREE (Figure 11), FLDVAR (Figure 12), FLDDUR (Figure 13), BFI (Figure 14), ZERODAY (Figure 15), LOWPRED (Figure 16), and LOWFREE (Figure 17). Less discrimination among clusters occurs when static basin descriptors are examined such as area (Figure 18), elevation (Figure 19), mean daily flow (Figure 20), and mean annual runoff (Figure 21).

The distinction between SN1 and SN2 clusters in the 816-site sample can be appreciated by examining the differences among clusters in terms of average timing of flood onset and elevation (Figs.19 and 22). SN1 sites tend to be at higher elevations, which probably contributes to greater seasonality through a more enduring snowpack, as indicated by a later seasonal onset of snowmelt (Figure 22). In practical terms, SN1 and SN2 could be lumped together to form a unitary SN group for the 816-site sample, since the ecological distinction among the two groups is subtle at best.

The distinction between SR1 and SR2 clusters in the 420-site sample cannot be easily discerned from the hydrologic variables or basin descriptors used in the study. However, SR1 streams tend to be lower elevation (Figure

TABLE 7. NUMERICAL MEANS AND STANDARD DEVIATIONS (IN PARENTHESES) OF 11 VARIABLES FOR 10
CLUSTERS FOR 816 GAUGED STREAM SITES. VARIABLES INDICATED BY "*" WERE NOT INCLUDED IN
THE TWO-STAGE CLUSTER ROUTINE AT ANY TIME, BUT ARE INCLUDED FOR COMPARATIVE PURPOSES.
FOR INTERMITTENT STREAMS, EXCLUDED VARIABLES ARE INDICATED BY "--"

	Perennial Runoff (PR)	Mesic Groundwater (GW)	Super Stable (SS)	Snow + Rain (SR)	Snowmelt (SN1)	Snowmelt (SN2)	Peren. Flashy (PF)	Intermit. Runoff (IR)	Intermit. Flashy (IF)	Harsh Intermit. (HI)
N	384	84	23	101	48	12	54	49	21	40
DAYCV	175.1 (53.8)	108.5 (37.9)	73.4 (49.3)	142.1 (41.9)	139.5 (29.1)	175.8 (27.8)	312.1 (89.9)	272.4 (82.9)	430.1 (100.1)	496.9 (192.3)
DAYPRED	55.4 (11.9)	72.0 (5.4)	74.4 (5.2)	68.4 (10.9)	77.6 (9.3)	58.7 (4.9)	33.8 (9.4)	31.7 (6.7)	20.6 (4.1)	48.9 (17.2)
BFI	8.3 (7.1)	29.5 (10.0)	51.3 (17.7)	10.4 (7.6)	15.2 (7.1)	9.7 (4.9)	3.5 (4.8)	--	--	--
ZERODAY	0.43 (1.3)	0.00 (0.00)	0 (0)	0.11 (0.90)	0.01 (0.06)	0.06 (0.16)	2.5 (2.9)	24.5 (12.4)	39.1 (18.6)	183.5 (68.4)
FLDFREQ	0.71 (0.20)	0.74 (0.15)	0.67 (0.09)	0.75 (0.18)	0.62 (0.11)	0.66 (0.10)	0.87 (0.14)	0.81 (0.17)	0.88 (0.17)	0.91 (0.25)
FLDVAR	0.29 (0.11)	0.29 (0.08)	0.29 (0.20)	0.28 (0.14)	0.32 (0.26)	0.29 (0.10)	0.53 (0.40)	0.40 (0.24)	0.45 (0.22)	0.48 (0.26)
FLDPRED	0.47 (0.12)	0.44 (0.10)	0.63 (0.12)	0.69 (0.10)	0.96 (0.08)	0.91 (0.11)	0.44 (0.09)	0.53 (0.14)	0.46 (0.10)	0.58 (0.13)
FLDFREE	0.24 (0.13)	0.19 (0.09)	0.39 (0.14)	0.53 (0.12)	0.77 (0.15)	0.74 (0.17)	0.21 (0.12)	0.36 (0.19)	0.19 (0.11)	0.42 (0.18)
FLDDUR	2.8 (2.2)	2.3 (1.5)	4.4 (2.8)	3.6 (2.4)	9.9 (2.7)	7.0 (1.7)	2.7 (1.3)	--	--	--
LOWPRED	0.74 (0.16)	0.65 (0.14)	0.45 (0.10)	0.81 (0.15)	0.76 (0.16)	0.57 (0.19)	0.54 (0.40)	0.65 (0.13)	0.49 (0.06)	0.4 (0.14)
LOWFREE	0.66 (0.17)	0.57 (0.16)	0.28 (0.09)	0.72 (0.15)	0.68 (0.16)	0.50 (0.16)	0.39 (0.19)	0.54 (0.19)	0.23 (0.10)	0.25 (0.15)
AREA*	916 (980)	757 (901)	1233 (1154)	804 (891)	969 (1112)	1082 (1549)	1041 (795)	754 (965)	997 (1027)	870 (1074)
QMEAN*	10.2 (11.1)	12.1 (13.2)	12.0 (10.5)	18.9 (9.0)	16.3 (22.0)	5.9 (24.6)	6.3 (24.6)	4.0 (6.1)	2.8 (3.9)	0.6 (0.7)
MAR*	0.46 (0.28)	0.58 (0.28)	0.40 (0.35)	1.06 (0.89)	0.48 (0.20)	0.27 (0.16)	0.20 (0.14)	0.27 (0.18)	0.14 (0.08)	0.05 (0.06)
POR*	42.4 (11.7)	42.5 (12.9)	47.6 (9.0)	39.3 (12.7)	39.2 (12.8)	37.3 (11.8)	40.3 (11.6)	35.7 (11.0)	40.6 (7.1)	29.8 (9.8)

19) and to have an earlier onset of flooding (Figure 22) than SR2 sites. This suggests that the SR1 group is very similar to Poff and Ward's (1989) "Winter Rain" streams, while the SR2 cluster more closely represents their "Snow+Rain" streams. Poff and Ward (1989) separated these two types of streams using a "flood timing" variable; however, their variable was not used here because they failed to take into account the underlying circular distribution of the seasonal variable. In short, a flood that occurs on day 10 of the water year is more similar seasonally to a flood occurring on day 364 than it is to a flood occurring on day 270, but standard statistical techniques will not detect this because they measure distance as a function of absolute difference (see Figure 22). Unfortunately, no single numerical representation can be used to indicate this circular relationship. However, inspection of Figure 22 shows that SR1 streams have median FLODTIME at day 81 of the water year, which is December 19, a time of heavy winter precipitation generated by Pacific storms. High elevation and inland SR streams (see below) have seasonal flooding more heavily influenced by snowmelt (median day = February 21).

Cluster Results: Geographic Distribution

The spatial distribution of the identified clusters shows reasonably good geographic affiliation. For the 420-site sample, PR streams occur primarily in the Eastern Deciduous Biome, with some representation in the West (Figure 23a). Stable GW streams also occur primarily in the East (Figure 23b). SS groundwater streams are largely restricted to the upper Midwest, although a few of them occur in the Northwest (Figure 23c). The SR streams are primarily in the Pacific Northwest (Figure 23d), although a significant portion of the SR2 streams are scattered across the northern tier of states. Some likely misclassifications occur in this group, as indicated by the identification of SR streams in the Southeast. The Snowmelt streams show high regional fidelity, being almost restricted to high elevation Rocky Mountain states (Figure 23e). The PF group also shows good regional affiliation for the forest-prairie transition of the Midwest (Figure 23f). A small group of PF streams also occur along the humid western Gulf Coast. The intermittent streams (HI, IR, IF) tend to occur in the arid Southwest and Great Plains, though some occurrences in the East are seen (Figure 23g).

For the 816-site sample, similar geographic patterns were observed. PR sites (Figure 24a) were mostly in the East, as were GW streams (Figure 24b).

SS sites remained predominantly upper midwestern in distribution (Figure 24c), and SR streams displayed a northwestern and northern-tier geographic pattern (Figure 24d). Snowmelt streams were mostly restricted to the Rocky Mountain region, but a noticeable proportion (7/12) of SN2 streams occurred in the upper Midwest (Figure 24e). Perennial Flashy streams retained a strong signature for the forest-prairie transition zone (Figure 24f). Among the intermittent stream types, HI streams were most strongly associated with the northern prairie, the southern prairie and the far southwest (Figure 24g). IF streams appeared to occur in the forest-prairie transition zone of the southern plains, while IR streams were more widespread, showing a more eastern, northern and far western distribution (Figure 24g).

Cluster Stability

It can be noted that when sample size was shifted from 420 to 816, some stream sites changed cluster affiliation (e.g., cf. PR streams in CA, NV, OR, and WA in Figs.8a and 9a). These "misclassifications" illustrate an important limitation to the use of cluster analysis or any other classification scheme: results are always relative to total variation expressed in the input matrix. Thus, because the total sample variability changes when the analysis is expanded from 420 to 816 streams, some sites will shift cluster membership because the among-site distances in multivariate space have been slightly altered. To assess the "robustness" of the clusters identified in the analysis of the 383 "permanent" streams, we employed a bootstrapping technique (see Methods). Based on 200 replicates, we found:

	Mean	5%tile	95%tile
$M_{r|o}$	.80	.69	.87
$M_{o|r}$	.54	.42	.68

This suggests that streams which originally clustered together tend to stay together (mean $M_{r|o}$ = .80), but that points which are together in the resample-based clusters do not necessarily share common original clusters (mean $M_{o|r}$ = .54). In other words, the resample clusters tended to join together several of the original clusters. Inspection of the resample clusters showed that original clusters PR, SS, SN, and PF (1, 5, 6 & 7) were

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reproducible, but that clusters GW, SR1, and SR2 (2, 3, & 4) often merged together into the PR group. These results indicate that the statistical separation between the PR, GW, and SR clusters is weak, and, on purely statistical grounds, these groups cannot be said to constitute discreet groupings. However, on *ecological* grounds, there is some justification for retaining these as separate groups. Given the importance of seasonality of flood regime, it is reasonable to accord FLDPRED a high weight in discriminating among clusters. Thus, the argument can be made that the average differences in FLDPRED and DAYPRED/DAYCV between the PR streams and the SR streams (particularly the SR2 streams) are of *ecological* interest, if not strict statistical significance. The geographic separation of the PR and SR sites further argues for their segregation (cf. Figure 23a and 23d). The differences between the PR and GW sites are less obvious. Clearly, the overlap for these clusters is great with the exception of DAYCV, PREDDAY, and BFI (see Table 6). These variables, however, are often used as primary discriminating variables in exploring hydrological-ecological relationships (see Section 3, this report), so it is not unreasonable to argue that there are *ecological* reasons for retaining the distinction between PR and GW streams. It should be emphasized here that the SS group is an extreme representation of the GW group, and the SS group did show statistical stability during the bootstrapping simulations.

DISCUSSION

Climate change that modifies local precipitation regime and that increases air temperature will modify the physical habitat template of a stream via an integrated catchment response in which vegetational, hydrological, thermal, and geomorphological components interactively adjust to the substantially altered conditions (Poff 1992a). As mentioned previously, the magnitude, frequency, duration and predictability of environmental extremes (flow, temperature) are viewed as agents of disturbance and hence important regulators of ecological processes and patterns in lotic systems (see Resh et al. 1988, Poff and Ward 1989, 1990 for extended discussions). Local community assembly and species persistence (including riparian vegetation) have presumably been influenced by the characteristic disturbance regime, such that frequently "disturbed" communities are relatively resilient

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(see Poff and Ward 1990, Reice et al. 1990, Schlosser 1990, Wallace 1990).
Given this argument, climate change that substantially alters the magnitudes
and temporal distribution of extreme events may be expected to have the
greatest relative impact on resident ecosystem structure and function. Thus,
historical variability regime becomes a relevant variable in projecting the
possible direct hydrologic consequences of specified climate change (see
Figures 9, 10). Over longer periods of time, if temperatures increase,
resident fauna may simply be removed as thermal tolerances are exceeded.
Presently, the geographical distribution of climate change cannot be
predicted, thus it is impossible to know where physical habitat templates may
be most severely modified. However, it seems likely that at biome boundaries,
where relatively rapid, coupled transitions in vegetation and precipitation
patterns occur, geomorphic systems may be near thresholds of change and
ecological systems may be most vulnerable.

Several types of stream responses to altered hydrologic regimes are
worthy of discussion. First, changes in the absolute amount of annual
precipitation will influence stream permanence. Several studies have shown
that, in arid-land streams particularly, large relative decreases in
streamflow are correlated with small absolute declines in precipitation
(Langbein 1949, Revelle and Waggoner 1983, Karl and Riebsame 1989).
Simulation studies have also emphasized this sensitivity (e.g., Flaschka et
al. 1987, Schaake 1990), and the ecological consequences of any systematic
reduction in flow in arid-land streams has been addressed by ecologists (Dahm
and Molles 1992, Grimm and Fisher 1992). Streams in cool and/or humid regions
do not exhibit substantial reductions in annual runoff with temperature
increases of ca. 1°C (Karl and Riebsame 1989), but severe reductions in
regional precipitation could clearly diminish average flow and push some
perennial streams into greater intermittency by increasing the number of days
with zero flow. For example, a fairly clear geographic break in the
distribution of perennial and intermittent streams corresponds to the forest-
prairie transition in the Midwest (cf. PR and PF streams to IR and IF streams
in Fig. 24). Climatic change that causes the Midwest to become drier and
encourages eastward progression of prairie would likely endanger many
permanent midwestern streams. However, a mitigating factor in this potential
response would be underlying geologic control on stream baseflow. In
particular, mesic groundwater and superstable streams would appear to be

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buffered against immediate negative responses to reduced precipitation inputs because of aquifer storage. These streams, which also are likely to have cooler summer thermal regimes due to groundwater inputs, might be viewed as providing significant regional refuges for biota threatened by increasing aridity and elevated air temperatures (cf. Meisner et al. 1988, Meisner 1990).

At present, predictions for regional climate responses to global warming cannot be given with confidence. Regional precipitation in climatically-distinct regions may change by ± 20% and runoff may change by ± 50% (Schneider et al. 1990). Regions that are now semi-arid may experience increased annual precipitation, thus allowing presently intermittent streams to become permanent. Such a change would represent a significant modification of the present hydrologic template, and resident lotic communities would presumably adjust in response to new habitat conditions.

A second major type of hydrologic change that could influence lotic communities is an altered regime of hydrologic *extremes*, the frequency and intensity of which are likely by-products of climatic change (Rind et al. 1989). For example, in stable groundwater-fed streams, more frequent flooding due to a more energetic atmosphere would increase overall flow variability. Since biotic interactions are presumably strong in streams having very stable hydrographs (see Meffe 1984, Schlosser 1987, Poff and Ward 1989), increased hydrologic variability would be expected (in theory) to modify community structure by favoring generalists and/or inferior competitors. In other types of streams, flashier hydrographs could result in major geomorphic changes that would directly modify habitat conditions for resident biota. There are several good paleohydrological and direct observational studies that clearly illustrate the important interaction between mean annual precipitation and flood regime in influencing channel morphology and geometry (see Schumm and Lichty 1963, Schumm 1968, Burkham 1972, Know 1972, Williams 1978). In general, mean annual precipitation controls the extent of vegetative cover and thus influences runoff and sediment supply rate, and catastrophic channel responses tend to result from frequent, intense flooding during periods of low annual precipitation and reduced vegetation. These rapid channel responses occur over a time scale of years under "normal" climatic fluctuations and are thus likely to be observed as global climate change progresses (see Poff 1992 for further discussion). Most of these changes have been documented in semi-arid areas; however, even in humid regions with their heavy vegetation cover

and relatively cohesive soils, intense storms may cause localized episodic channel widening (Costa 1974) or erosion (Kochel 1988).

A third important ecological consequence of climatic change on stream hydrology will result from altered *seasonality* of extreme events. The most likely mechanism producing this response is increased temperature that reduces the amount of time that frozen precipitation remains in storage as snowpack. Several simulation studies have shown how moderate increases in annual temperatures can cause early onset of snowmelt and lead to winter flooding (e.g., Gleick 1987, Lettenmaier and Gan 1990, Schaake 1990). High altitude and latitude streams may shift from highly seasonal, primarily snowmelt-driven systems to more variable snow+rain streams with more predominant winter floods. Similarly, snow+rain streams might shift to entirely rainfall-dominated systems with no seasonal storage of precipitation. Flood predictability and timing may be important environmental correlates of spawning and recruitment success (e.g., Seegrist and Gard 1972, Nesler et al. 1988), so changes in seasonality of high flows can be expected to produce strong ecological responses. An additional consequence of a potential shift from snowmelt to rainfall-dominated systems is that many snowmelt streams occur in semi-arid regions where late summer baseflow is provided by the slow melting of the lingering snowpack. Early melting of snowpacks, if not accompanied by an increase in summer precipitation, will result in a tendency for late summer drying and a loss of habitat for present communities. Another consequence of warmer winter temperatures might be loss of extensive seasonal ice cover, which often serves to limit diversity and abundance of fish species in small, northern streams (Schlosser 1987).

A problem with any speculative projection about how climate change may affect hydrologic regimes and hence lotic communities is that systematic streamflow data extend only on the order of decades into the past. The natural variability in climate makes even detection of trends in hydrologic means very difficult (Karl 1988, Matalas 1990) and ensures that the prospect of statistically documenting regional climate change will remain uncertain for several decades (Schneider et al. 1990). Further, the assumption of temporal invariance in hydrologic events is likely to be invalid under a changing climate, such that prediction of spatial and temporal distribution of hydrologic means and extremes based on empirical records will be dubious (Moss

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and Lins 1989). All these considerations mitigate against unconditional "predications" about regional hydrologic responses to climate change.

Beyond the concern for prediction of changes in the physical environment is the great uncertainty associated with establishing robust relationships between hydrologic regimes and ecological patterns and processes. Much present theory in stream ecology emphasizes the regulatory role that hydrology and disturbance regime play in organizing community structure and constraining species distributions and abundances (see overviews in Resh et al. 1988, Poff and Ward 1989, 1990, Minshall 1988, Fisher and Grimm 1992). However, compelling empirical data linking ecological organization to hydrologic regime are largely lacking because the appropriate large-scale "controlled" ecological comparisons have not been done (but see Section 3). Thus, any "predictions" about the ecological consequences of climatic change must explicitly acknowledge a high degree of uncertainty in the knowledge base.

Despite the uncertainties of both hydrological and ecological prediction, it is important for stream ecologists to have a "phenomenology" of streamflow types in order to better appreciate the existing range of hydrologic variability in North American streams and rivers. The typology presented in this paper is based on ecologically-relevant hydrologic attributes; therefore, it can be expected to provide a meaningful basis for identifying streams that differ in major aspects of ecological organization. An objective framework that allows comparable sites to be matched and establishes reasonable a priori expectation is required to enhance potential success of research and management of climatic change.

CONCLUSIONS

Relatively undisturbed U.S. streams were classified according to variation in 11 ecologically-relevant hydrologic characteristics. A group of 420 "best" stream sites and a group of 816 "acceptable" sites (including the 420 best sites) were evaluated with similar results. Cluster analysis resulted in the identification of 10 distinctly different stream types. Most of these stream types exhibit reasonable geographic affiliation and can be interpreted in terms of regional climatic patterns and local variation in geologic characteristics. Four of the seven perennial stream groups (PR, SS, SN, and PF) were found to be robustly defined when subjected to a

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bootstrapping technique. The other three groups (GW, SR1, and SR2) typically merged together into the PR group and are thus not statistically distinct. However, these groups can probably be retained on ecological grounds, because of their inherent differences in flood predictability and baseflow characteristics.

The derived classification for *U.S.* streams based on ecologically-relevant hydrologic characteristics provides a comprehensive catalog that identifies streams that, according to ecological theory, may differ in major aspects of ecological organization. This classification thus provides a basis for hypothesis-generation and affords an objective framework for matching streams for purposes of comparative ecological investigations. Moreover, this hydrologic classification can be used to assess the *potential* ecological consequences of hydrologic changes, because specific kinds of hydrologic change induced by climatic changes (e.g., increased intermittency, reduced flood seasonality, etc.) can be compared to the historical hydrologic patterns summarized in this classification.

SECTION 2

IMPORTANCE OF TEMPORAL SCALE IN ASSESSING STREAMFLOW PREDICTABILITY
AND FLOOD REGIME IN STREAMS OF DIFFERENT GEOGRAPHIC AREAS

INTRODUCTION

A growing need in stream ecology is the establishment of criteria with
which study sites can be selected for comparative work (e.g., Fisher and Grimm
1991). Stream ecologists have relied on criteria such as stream order and
trophic base (e.g., Vannote et al. 1980) or ecoregions (Omernik 1987).
Increasingly, similarity in hydrologic regime is seen as an important
criterion for site matching because hydrologic events play important
structuring role in stream ecosystems (Resh et al. 1988). Indeed, there are
now several examples of comparative hydrologic analyses that ecologists may
use to guide site selection for biological studies (e.g., Resh et al. 1988,
Poff and Ward 1989, Hughes and James 1989, Jowett and Duncan 1991).

Several papers over the past few years have shown the great variation in
hydrologic regimes that exists among streams at regional and continental
scales at a variety of locations throughout the world (see Section 1 of this
report for a summary). Classification of streams having similar hydrology can
certainly assist in proper site-matching; however, the criteria by which
different researchers classify streams are variable and often based on non-
formal or ad hoc statistical descriptors of hydrologic variation. Implicit in
any hydrographic analysis is the treatment of temporal scale. The length of
the hydrologic time series is an obvious factor that determines what kinds of
statistical summaries can be extracted from the data. Less obviously, the
temporal resolution with which the available data are viewed can influence the
interpretation of the derived statistical summaries. Hydrographs can be
analyzed with numerous degrees of temporal resolution, and the scale chosen
typically reflects specific interest in hydrologic phenomena having different
periodicities. For example, an annual time scale may be appropriate if the
question involves assessing inter-annual variation in spring runoff (e.g.,
Molles and Dahm 1990). Intra-annual seasonal patterns of hydrologic variation
might be assessed with monthly data (Resh et al. 1988, Bunn et al. 1986).

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Transient events, like spates, may require high resolution, daily data (Poff and Ward 1989).

Approaches to comparing the hydrologic similarity of lotic ecosystems are relatively new, and no "standardized" methods have been accepted with which to proceed. A necessary first step toward this end is determining whether available methodologies can be unambiguously applied under a range of circumstances that are likely to be encountered in applying the methodology to actual problems. An important aspect of this effort is to examine how robust the methodologies are to variation in the temporal resolution with which the data are viewed. If standard methodologies provide different answers depending on the scale of observation and analysis, then those limitations need to be acknowledged and taken into account when applying the methodologies. Thus, the issue of scale-dependency in pattern analysis is very important for ecologists interested in using hydrologic records to establish "comparable" sites for biological studies.

There are two objectives in this section. First, we wanted to examine how sensitive a widely-used, formal measure of predictability (Colwell's index) is to variation in the size of the temporal window with which the raw data are initially viewed. Second, we wanted to focus on the question of what degree of temporal resolution in a hydrologic dataset is required to adequately describe the occurrence of extreme high flows. A further aspect for both of these objectives was our interest in examining the geographic variation in sensitivities to temporal scale of analysis. Therefore, a large number of streams representing a wide range of climatic regions were selected from across the continental United States.

Colwell (1974) introduced a formal measure of environmental predictability that has received widespread use in many stream ecological studies over the last several years (Resh et al. 1988, Poff and Ward 1989, see Gordon et al. 1992). This method essentially reconfigures a data time series into a two-dimensional matrix consisting of n states by p time intervals. The states are merely categories of discharge level. The time intervals are divisions of some natural period, typically an annual cycle. For example, a long time series of annual hydrologic data could be broken into time intervals of months, weeks, days, etc. Colwell's index is quantitative, yet it has several drawbacks. First, there are no objective criteria for establishing the number of discharge levels used to calculate the index, and the calculated

value is sensitive to variation in this parameter (Gan et al. 1991). Second, the index value is sensitive to length of hydrologic data record, requiring about 40 years of continuous record to produce a stable output (Gan et al. 1991). Third, the partitioning of the time scale is arbitrary. Individual researchers have calculated Colwell's index using monthly (Resh et al. 1988, Gan et al. 1991, Bunn et al. 1986) and daily (Poff and Ward 1989) time scales. The consequences of arbitrary temporal resolution in the definition of time scale using Colwell's index have not been explored.

Hydrologic extremes are recognized for the control they exert on stream communities, and a host of important ecological questions arise from considering the temporal distribution (regime) of such extremes (see Resh et al. 1988, Poff 1992). Yet there is no consensus as to what degree of temporal resolution in hydrologic data is required to adequately characterize a stream's spate regime. If monthly data are as useful as daily data in allowing the accurate description of the frequency and predictability of extreme events, then the task of site matching is made much easier, because monthly data are generally more accessible and can be more easily extrapolated from readily available precipitation data. However, situations may arise where average monthly flow does not correlate with flood events because large, transient floods leave little signature on the monthly average. Similarly, annual flow data can be misleading in terms of inferring spate regimes because dry years may be dry on average, but have significant spates (e.g., Grimm 1992). The adequacy of using coarse grain or aggregated hydrologic data (e.g., monthly, annual) to make inferences about transient hydrologic phenomena such as floods may vary among streams depending on total precipitation or local catchment geology. For example, intermittent streams may be less sensitive than perennial streams to changes in time scale used to characterize flood regimes because a large flood in an intermittent stream may leave a permanent signature on the monthly average. Similarly, highly seasonal streamflow regimes, such as those dominated by snowmelt, may not require fine grain data to characterize the distribution of extremely high flows accurately. The temporal scale of hydrologic data needed to characterize floods and the geographic variability of this characterization has not received previous attention in the stream ecology literature.

METHODS

Data were taken from long-term U.S.Geological Survey flow records using the methods described in Section 1 of this report. All sites represented flow regimes relatively unimpaired by anthropogenic modifications. Additionally, each site was evaluated for a 36 yr period (1950-1985), a length of time sufficient to allow a stable estimate for Colwell's index of predictability (see Gan et al. 1991). In an earlier analysis, a total of 480 sites were selected and analyzed using non-hierarchical cluster analysis for a streamflow classification (see Section 1). All sites in this analysis met the 36-yr criterion. Each of the 10 groups resulting from the classification was "subsampled" to provide data for the present analysis. No more than 12 sites per classification group were selected for a total sample size of 118 gauged streams. Sites were not randomly subsampled from the initial classification groups. Rather, for each of the 10 groups, the sites closest to the multivariate centroid of the group were selected by inspection to insure that the sample would represent the sites most characteristic of each group. The 10 groups themselves essentially span the range of hydrologic variability available in the best available hydrologic data set for the entire U.S. Selecting the sites in this manner allowed us to examine the entire range of hydrologic variability and to test for significant differences among previously-defined hydrological types. An additional two groups were defined because two of the original 10 groups had members that occurred both in the eastern and the western U.S., two broadly-defined regions which differ in climatic seasonality. These two groups were partitioned geographically (for a total of 12 groups) so we could evaluate the extent to which the classification results were robust against geographic location.

Colwell's Index

The input for calculation of Colwell's index was the daily hydrograph. All hydrographs were organized according to the "water year", which commences on October 1 and ends on September 30 of the following calendar year. Data were standardized by dividing each entry in the matrix by the overall mean value of the matrix. This allows streams of different sizes to be directly compared. Nine class intervals (states) were used for discharge, and they were bounded at the following increments of $\log_{10}$ units: -1.5, -1.0, -0.5, 0,

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0.5, 1.0, 1.5, 2.0. These categories span the range from <0.03 to >100 times the average flow (on an arithmetic scale). The number of flow states selected can influence the calculation of predictability (Gan et al. 1991), yet there is no objective criterion for selection of the number of states or their scaling (see Gordon et al. 1992). We chose these nine flow states to span a wide enough range to capture "extreme" events that occurred for the entire range of data under consideration.

Separate indices of predictability at each site were determined for four time steps that comprise segments of the annual cycle: daily, weekly, monthly and seasonal. Our hypothesis was that calculated predictability values would not vary within the 12 streamflow types as a function of temporal scale used to calculate the value. These four intervals span the range of temporal frames with which stream ecologists generally work. For each site, a daily matrix consisted of 365 days x 36 yr of data. Day 366 of leap years was omitted. The weekly matrix was derived by taking the average weekly flow for 52 7-d periods for each of the 36 yr. Days 365 and 366 (in leap years) were omitted. The monthly matrix was derived by determining the average flow for each calendar month of the year. The seasonal matrix consisted of four, 3-month "seasons", starting with October.

Importance of temporal scale in assessing spates

To determine how effectively hydrographic data of coarse temporal resolution can assess transient events (spates) in streams, we compared monthly and annual flow statistics to daily flow statistics. If coarse grain data (e.g., monthly to annual) are capable of allowing detection of transient events, then, at a minimum, the signatures of the maximum daily (instantaneous) flow ought to be present in the time series of the coarse grain data. For the *monthly* time scale, we determined for each of the 36 years the month having the highest average flow. Using the daily flow matrix, we then recorded for each year the month in which the highest daily flow occurred. We calculated the proportion of the 36 observations where the high monthly flow and the month of highest daily flow matched. For example, a stream with the highest daily flow each year in the same month having the highest average monthly flow would score a maximum proportion of 1.0. Differences among the 12 groups were tested with respect to proportion of

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TABLE 8. ABBREVIATIONS AND SAMPLE SIZES FOR 12 DIFFERENT CLASSIFICATION GROUPS USED IN THE ANALYSIS

Descriptive Title	Abbreviation		sample size
Perennial Runoff	PR1	(East)	11
	PR2	(West)	11
Stable Groundwater	GW1	(East)	11
	GW2	(West)	4
Superstable Groundwater	SS		12
Snow + Rain	SR1	(Type 1)	9
	SR2	(Type 2)	12
Snowmelt	SN		11
Perennial Flashy	PF		12
Intermittent Runoff	IR		10
Intermittent Flashy	IF		9
Harsh Intermittent	HI		6

matched flow events after arcsine transformation with one-way ANOVA and Student-Newman-Keuls multiple comparison tests (SAS 1988).

The utility of *annual* flow data in assessing peak daily flows was assessed using rank correlation. For each year in the 36-yr record, the series for both the maximum daily flows and for the annual average flows were ranked (allowing for ties). Spearman's rank correlation coefficient (r_S) was determined for the ranks of these two series. The null hypothesis of no positive correlation between the daily and annual series for each individual stream site was tested using a one-tailed Spearman's ρ (Conover 1971, p. 248). Differences among the 12 groups with respect to average rank correlation were examined after arcsine transformation with one-way ANOVA and Student-Newman-Keuls multiple comparison tests (SAS 1988).

RESULTS

The 12 groups used for the analysis are defined in Table 8. The 118 individual stream sites used in the analysis, and their scores for the various derived variables, are provided in Table 9.

Colwell's Index

Differences among Groups for a Fixed Time Step--

Clear differences among the 12 identified groups were found in terms of flow predictability at all temporal scales. For all four time steps, significant among-group differences existed at $p < 0.0001$. Figure 25 summarizes the differences among the 12 groups for each of the time steps used to calculate streamflow predictability. At the shortest (daily) time step, superstable (SS) and snowmelt (SN) streams had highest predictability values, while perennial flashy (PF), intermittent runoff (IR), and intermittent flashy (IF) streams had the lowest predictability values (Figure 25). For the longest (seasonal) time step, SS and SN streams retained the highest predictability values, but eastern groundwater (GW1) and high elevation snow+rain (SR2) streams were a close second. The lowest predictability scores were recorded for the IF, IR, and PF streams, in addition to the harsh intermittent (HI) streams.

The null hypothesis that all group means were equal was tested with oneway ANOVA for each of the four predictability time steps. In each case the null hypothesis was rejected at $p < 0.0001$. Significant pairwise differences among groups were examined for each predictability measure using the SNK multiple comparisons test (SAS 1988). These results are given in Table 10 and they correspond directly to Figure 25. Several interesting observations can be made. For example, the following pairs of groups were always statistically similar for all four predictability time steps: SN and SS, SR1 and GW2, GW2 and PR2, GW1 and GW2. The three groups in the triplet of PF, IR and IF were also statistically indistinguishable for all time steps. PR1 and PR2 streams were the same only for the monthly and seasonal time steps, while SR1 and SR2 streams were always different. Interestingly, the eastern perennial runoff (PR1) and stable groundwater (GW1) streams were always different from one another, whereas the western PR2 and GW2 streams were always the same (see below).

TABLE 9. SUMMARY OF 6 CATEGORIES OF STATISTICAL DATA DERIVED FOR 118 SITES
OVER A COMMON 36-YR PERIOD, BY STATE ABBREVIATION,
GAUGED STREAM NUMBER, AND FLOW GROUP AFFILIATION.

State	Gauge#	Group	Day-Month Matches	Day-Year r-value*	Predictability of Streamflow Day	Week	Month	Season
WV	03198500	PR1	55.56	0.677	43.75	45.55	52.54	62.52
PA	03102500	PR1	55.56	0.509	48.30	49.47	56.34	67.53
VA	02017500	PR1	63.89	0.424	51.76	51.92	57.71	69.18
NY	01350000	PR1	61.11	0.785	45.38	44.94	51.05	60.43
ME	01055000	PR1	50.00	0.481	50.53	51.34	56.79	70.52
IL	03345500	PR1	83.33	0.786	33.83	33.81	36.92	43.89
MN	04014500	PR1	69.44	0.388	47.16	48.13	53.16	58.35
IN	03334500	PR1	58.33	0.492	50.57	49.74	52.10	63.31
IA	06808500	PR1	69.44	0.502	42.02	42.95	46.26	48.52
LA	07352000	PR1	66.67	0.694	41.74	42.79	45.22	53.40
FL	02231000	PR1	80.56	0.625	35.23	35.80	37.24	42.70
CA	11315000	PR2	36.11	0.769	54.16	54.12	53.63	49.46
CA	11264500	PR2	63.89	0.887	48.08	48.48	51.73	55.40
NM	07203000	PR2	66.67	0.456	39.57	40.83	45.72	49.67
CA	11282000	PR2	55.56	0.922	45.23	45.19	46.92	45.64
CA	11266500	PR2	47.22	0.910	49.63	49.60	51.39	54.25
NM	07218000	PR2	44.44	0.810	41.48	42.17	43.96	46.85
CA	11230500	PR2	69.44	0.837	55.83	56.43	58.41	65.35
NM	08380500	PR2	58.33	0.662	45.75	46.20	47.63	49.78
NV	10329500	PR2	38.89	0.879	68.18	67.80	66.50	69.72
OR	14020000	PR2	41.67	0.713	69.29	69.79	73.29	81.15
WA	12186000	PR2	30.56	0.569	63.62	66.28	73.02	78.21
MO	07067000	GW1	77.78	0.614	65.81	64.89	66.19	70.60
GA	02217500	GW1	75.00	0.642	60.86	61.50	66.30	74.75
IN	04094000	GW1	55.56	0.772	69.53	68.82	74.22	77.91
AL	02374500	GW1	58.33	0.661	60.77	61.95	67.72	71.59
FL	02376500	GW1	77.78	0.577	68.64	68.18	69.88	73.55
VA	03170000	GW1	63.89	0.523	63.71	65.65	72.24	75.65
MD	01583500	GW1	61.11	0.546	60.94	61.94	63.94	68.09
IL	05438500	GW1	91.67	0.889	50.60	50.76	53.02	55.87
NC	02111000	GW1	44.44	0.319	60.95	61.18	65.04	67.12
PA	01555000	GW1	41.67	0.675	54.76	55.60	60.12	68.48
NJ	01396500	GW1	58.33	0.721	58.68	60.30	64.41	68.87
CA	11381500	GW2	61.11	0.855	64.40	64.26	66.49	73.13
NM	09430500	GW2	72.22	0.805	61.96	61.66	60.07	59.07
CA	11383500	GW2	58.33	0.818	59.63	59.66	60.84	63.35
TX	08172000	GW2	69.44	0.736	51.45	50.78	49.76	52.83
IL	05435500	SS	69.44	0.655	59.39	60.06	63.80	64.58
WI	05379500	SS	75.00	0.398	70.55	69.83	70.42	70.94
WI	05434500	SS	75.00	0.623	59.23	59.88	63.41	65.16
MI	04033000	SS	72.22	0.627	78.37	78.66	81.25	83.69
OR	14328000	SS	47.22	0.597	78.64	78.71	79.64	79.91
WI	04071000	SS	69.44	0.590	76.65	76.90	78.30	84.91
MN	05286000	SS	83.33	0.806	55.47	55.58	54.76	57.18
OR	14010000	SS	41.67	0.621	82.77	83.42	84.38	84.91
SD	06409000	SS	66.67	0.532	72.89	73.83	74.19	75.16
CA	11367500	SS	50.00	0.816	77.18	77.11	77.09	76.84

FL	02359500	SS	61.11	0.651	70.14	69.81	69.46	69.26
CA	11355500	SS	47.22	0.766	74.05	73.86	73.90	72.27
NV	10316500	SR1	83.33	0.846	63.31	63.91	66.26	65.13
OR	14325000	SR1	63.89	0.739	52.99	54.30	60.94	79.03
CA	11402000	SR1	58.33	0.845	54.64	54.95	56.08	57.65
OR	14042500	SR1	55.56	0.737	53.71	54.81	58.48	64.41
CA	11532500	SR1	63.89	0.609	59.81	60.03	65.08	72.76
WA	12020000	SR1	61.11	0.681	58.18	59.85	66.24	85.06
OR	14308000	SR1	58.33	0.702	58.81	60.09	64.98	65.12
CA	11382000	SR1	66.67	0.862	49.42	49.45	50.47	52.52
OR	14193000	SR1	72.22	0.475	62.74	63.80	68.17	77.83
WA	12488500	SR2	72.22	0.517	63.70	63.43	65.69	72.44
WI	05405000	SR2	77.78	0.449	65.36	66.90	69.09	70.85
OR	10396000	SR2	50.00	0.810	62.25	62.88	65.75	68.69
ME	01022500	SR2	52.78	0.583	54.92	56.63	60.45	68.01
MN	05275000	SR2	77.78	0.790	58.60	58.76	60.11	62.82
CA	11522500	SR2	52.78	0.714	57.24	57.87	61.90	66.88
WA	12451000	SR2	77.78	0.701	68.26	69.36	72.03	75.78
NY	04256000	SR2	75.00	0.474	59.12	60.20	64.98	77.15
OR	14179000	SR2	55.56	0.533	64.51	65.51	70.48	70.13
WA	12035000	SR2	72.22	0.496	67.32	69.25	76.78	90.17
MI	04105000	SR2	63.89	0.772	62.30	62.85	65.95	72.43
ID	12413000	SR2	72.22	0.678	64.76	65.26	67.74	70.19
ID	13120000	SN	80.56	0.886	74.92	75.67	76.85	78.01
MT	12332000	SN	75.00	0.708	72.26	73.73	76.27	76.30
ID	13336500	SN	86.11	0.665	68.22	68.97	70.47	71.09
MT	12358500	SN	83.33	0.717	68.43	69.52	71.74	76.12
CO	09112500	SN	83.33	0.914	74.95	75.07	76.59	76.14
ID	13120500	SN	83.33	0.860	71.45	72.34	74.60	76.18
CO	09124500	SN	86.11	0.840	75.00	75.71	77.66	80.03
MT	12355500	SN	86.11	0.718	71.15	71.95	72.68	77.60
ME	01013500	SN	80.56	0.692	55.58	55.57	56.02	64.78
MT	06207500	SN	88.89	0.721	70.16	70.95	74.33	83.14
CO	07083000	SN	80.56	0.869	72.84	73.38	76.28	80.74
MO	05498000	PF	72.22	0.744	29.96	27.48	27.15	34.44
IA	05486490	PF	61.11	0.686	28.73	28.27	29.92	38.38
MO	05500000	PF	55.56	0.832	29.04	27.26	28.56	36.19
IA	06898000	PF	66.67	0.771	28.07	27.47	29.03	36.63
IL	03346000	PF	75.00	0.743	31.77	30.07	31.49	40.07
TX	08070000	PF	72.22	0.835	39.92	37.75	36.39	38.92
TX	08068520	PF	83.33	0.881	34.24	32.12	31.66	34.48
SD	06481500	PF	77.78	0.904	32.80	32.26	31.39	29.24
KS	06892000	PF	66.67	0.828	28.13	26.47	27.84	32.09
NE	06811500	PF	77.78	0.794	44.18	41.66	43.13	46.75
LA	08010000	PF	66.67	0.662	27.45	27.30	39.62	55.54
CA	11063500	PF	83.33	0.716	33.93	33.36	33.09	33.17
AR	07261500	IR	72.22	0.712	37.72	35.93	38.19	44.88
CA	11098000	IR	80.56	0.923	36.95	35.91	36.50	36.65
SD	06356500	IR	72.22	0.872	46.36	46.16	48.95	51.94
KY	03298000	IR	66.67	0.592	36.34	34.02	36.68	49.57
ND	06354500	IR	83.33	0.921	40.32	39.99	40.38	33.93
ND	05066500	IR	88.89	0.949	40.27	39.92	38.77	33.28
KY	03320500	IR	66.67	0.659	37.29	36.46	42.14	49.06
MN	05300000	IR	83.33	0.878	35.56	35.40	34.59	32.59
CA	11111500	IR	75.00	0.928	42.80	41.64	38.25	36.91
KS	06917000	IR	66.67	0.792	32.52	29.87	27.69	30.10
KS	07167500	IF	69.44	0.804	31.91	29.18	29.04	29.19
KS	06911500	IF	66.67	0.802	33.67	30.59	28.80	30.92

OK	07311500	IF	83.33	0.793	43.39	37.54	27.83	27.73
KS	07180500	IF	72.22	0.684	31.84	29.13	28.02	30.96
AZ	09480000	IF	69.44	0.895	34.67	33.22	32.37	34.37
KS	06914000	IF	80.56	0.809	32.98	29.45	27.94	31.25
KS	07172000	IF	75.00	0.764	30.44	28.67	25.95	28.29
KS	06889500	IF	72.22	0.814	28.71	27.33	28.61	32.47
NM	08408500	IF	83.33	0.897	45.81	42.27	39.28	42.05
SD	06425500	HI	88.89	0.935	51.05	50.17	44.87	36.40
CA	11274500	HI	69.44	0.927	67.29	65.80	61.66	49.63
ND	05060500	HI	91.67	0.919	58.41	57.46	53.63	36.55
NM	07222500	HI	80.56	0.786	52.68	49.46	43.39	39.41
CA	11124500	HI	83.33	0.944	45.80	44.46	41.80	39.79
CA	10258500	HI	75.00	0.841	53.82	50.98	43.72	32.55

* $r_S > 0.55$ is significant at a = 0.001; $r_S > 0.30$ is significant at a = 0.05.

Differences within Groups for Variable Time Steps--

The 12 groups fell into three categories. First, some groups showed an *increase* in the estimate of predictability as time scale increased from daily to seasonal. Included in this group were SN, SR1, SR2, GW1, PR1, and PF streams (Figure 26). A second category of four stream types showed no discernible change in predictability with increasing time scale. Streams included in this category included PR2, GW2, SS and IR streams (Figure 27). The third category consisted of two groups of streams that were characterized by declining predictability values as temporal scale increased (Figure 27, bottom panels). IF streams predictability values reached a minimum at the monthly time step before increasing again at the seasonal time step. HI streams consistently declined and were thus the only stream type that had the lowest predictability at the longest time scale.

Importance of temporal scale in assessing spates

Daily vs. Monthly Data--

The correspondence between months with highest average flow and months with highest daily flow ranged from 30-90% across the 12 groups (Figure 28a). The groups with the greatest percentage of concurrence were SN and HI streams, both of which had median scores > 80%. All other groups had medians > 60%, with the exception of PR2 streams, which had a median score < 50%. Many of

TABLE 10. SUMMARY OF COMPARISONS OF SIGNIFICANT DIFFERENCES AMONG CLUSTER MEANS FOR ONEWAY ANALYSES OF VARIANCE FOR FOUR MEASURES OF OVERALL PREDICTABILITY OF STREAMFLOW (DAILY, WEEKLY, MONTHLY, AND SEASONALLY), FOR NUMBER OF MATCHES BETWEEN MAXIMUM MONTHLY AVERAGE AND MONTH WITH MAXIMUM DAILY FLOW, AND FOR RANK CORRELATION BETWEEN ANNUAL PEAK DAILY FLOWS AND ANNUAL AVERAGE FLOW. FOR EACH TEST, THE 12 CLUSTERS ARE ARRANGED FROM LEFT TO RIGHT IN DESCENDING ORDER OF CLUSTER MEAN SCORE. CLUSTER MEANS THAT ARE NOT SIGNIFICANTLY DIFFERENT FROM ONE ANOTHER (SNK TEST, $\alpha = 0.05$) HAVE A COMMON UNDERLINE. SIGNIFICANTLY DIFFERENT CLUSTERS HAVE DIFFERENT UNDERLINES. CLUSTER ABBREVIATIONS AND SAMPLE SIZES ARE GIVEN IN TABLE 8

Daily Predictability

```
SS    SN    SR2   GW1   GW2   SR1   HI    PR2   PR1   IR    IF    PF
--------  ------------------------------        ----------
                --------------------------------        ---------------
```

Weekly Predictability

```
SS    SN    SR2   GW1   GW2   SR1   PR2   HI    PR1   IR    IF    PF
--------  ----------------------------        ---         ---------------
                ------------------------
```

Monthly Predictability

```
SN    SS    SR2   GW1   SR1   GW2   PR2   PR1   HI    IR    PF    IF
------------------------------    ----------------        ---------------
          --------------------------    ----------------------
```

Seasonal Predictability

```
SN    SS    SR2   GW1   SR1   GW2   PR2   PR1   IR    HI    PF    IF
------------------------------    ----------------    --------------------
          ----------------
```

Day-Month Matches

```
SN    HI    IR    IF    PF    SR2   GW1   PR1   GW2   SR1   SS    PR2
------------------------------
          ------------------------------------------------------------
                      ------------------------------------------------------
```

Rank-Correlation

```
HI    IR    IF    GW2   SN    PF    PR2   SR1   SS    GW1   SR2   PR1
------------------------------------------    ----------------------------
          --------------------------------------------------------
              ----------------------------------------
```

these groups were significantly different at $\alpha = 0.05$ using the SNK multiple comparisons test (Table 10).

Daily vs. Annual Data--

When the rank correlations between the series of annual maximum daily flow and annual mean flows were determined, values ranging from 0.32 to 0.95 were observed (Table 9, Figure 28b). For a sample size of 36, a r_s value > 0.30 was significant at $\alpha = 0.05$; therefore, all individual stream sites had significant correlations between annual maximum and annual average flows. For all 12 stream groups, medians exceeded 0.6, with the exception of PR1 streams. HI streams were the only group with a median exceeding 0.9. Although there was ample overlap among groups, some statistically significant differences were found (Table 10). One interesting pattern was that the western perennial runoff and stable groundwater streams (PR2 and GW2) had significantly greater correlations between maximum annual average and maximum annual daily flow (Figure 28b). For the perennial runoff streams, at least, this pattern was the opposite of that observed for the daily-monthly matches (Figure 28b), where eastern PR streams were less sensitive to a change in time scale than their western "counterparts".

DISCUSSION

This analysis shows that the temporal scale with which one analyzes a hydrologic time series has significant implications for the inferences drawn about streamflow predictability and disturbance (spate) regime. The magnitude of the "impact" of using different scales varies with geographic location, so any comparative hydrologic analysis at a regional or larger scale should take these relationships into consideration.

The results from the repeated calculation of Colwell's index of predictability applied to streamflow records for the 12 groups of streams identified here show two things. First, there are generally large among-group differences regardless of what temporal scale is used. This fact allows us to identify "types" of streams that are in a sense independent of the scale that is chosen. For example, snowmelt streams have very high predictability relative to most other stream types, regardless of whether predictability is calculated with daily, weekly, monthly, or seasonal data. Therefore, as long

as temporal grain is consistent, it is possible to discern major differences in predictability for a wide range of hydrologically diverse streams.

Second, within certain groups, significant changes in the estimates of predictability occur, *depending* on the time scale chosen. For some groups, predictability increases, for others it stays the same, and for others, declines occur. These substantial changes can even exceed the among-group differences (cf. HI in Figure 25). These observations suggest that, when comparing measures of predictability among hydrologically and/or geographically diverse streams, one should give due consideration to the rationale for choosing a particular temporal window for analysis.

Third, there appears to be a geographic signature on the calculation of predictability that to some extent overrides the importance of streamflow classification type. The eastern PR1 and GW1 streams were always different in terms of mean predictability at different time scales (see Figure 25, Table 10); however, the western PR2 and GW2 streams were never statistically distinguishable. This finding suggests that only in the eastern U.S. are these two stream types easily separable (where they are most abundant). Runoff streams appear to respond rapidly to precipitation events whereas stable groundwater streams are presumably less responsive due to substantial aquifer storage. In a climate where significant precipitation can occur at any time of the year (i.e., eastern U.S.), PR streams would exhibit frequent discharge fluctuations in response to precipitation, but under a strongly seasonal precipitation regime (as in the West), streamflow variation in PR streams would be more seasonal and hence less sensitive to temporal scale chosen to estimate predictability.

For estimation of the flood regime, our results show that coarse-grain data can be used if one is willing to accept a high error rate. For certain streams (SN), monthly data can be used to identify the month of the year with the maximum single daily flow with up to 80% accuracy. However, for others (e.g., PR2) the correspondence is less than 50%. These results caution against using monthly flow data to accurately characterize the spate regimes for most streams. Many streams experience high flows of ecological significance more than once per year, and as the number of high flows of interest increases, it is increasingly unlikely that monthly data can adequately capture the temporal distribution of those transient but important events. By contrast, monthly data are probably adequate for analysis of

lowflow events (which we did not analyze here), because lowflow events are generally of greater duration than high flow events.

The two groups with the highest day-month match were SN and HI streams. Given the high seasonality of high flows in snowmelt streams, it is not surprising that these streams would be relatively insensitive to the temporal scales used in this study. The high correspondence across temporal scales for harsh intermittent streams can probably be explained by considering that these streams are defined as having zero flow for at least half of each year, on average. Thus, any large flow occurring in these streams, however transient, will probably make a significant contribution to flow values averaged over longer time scales.

The rank correlations between the series of annual average flows and annual maximum daily flows were always statistically significant ($p < 0.05$) for individual streams (r_S with 35 d.f. > 0.30). This suggests that annual flow data might be useful in reconstructing hydrologic extremes for some types of streams for which only annual flow data exist or for which only precipitation data exist. However, the low *absolute* value of the rank correlations for most streams indicates that the relationship between high annual flows and high flow years contains substantial scatter. Further, the correlations provided do not take into account the possibility that, in particular years, several high flows may occur that exceed the magnitude of even the highest annual flow of some other years. Thus, the information contained in the rank correlation structure cannot be used reliably to describe the *frequency* of flooding of a particular intensity for many stream types. However, for highly seasonal streams (e.g., snowmelt), where maximum annual flows almost always occur at a particular time of year (during snowmelt), average annual flow statistics may provide very useful information in determining magnitudes of major flows on a yearly basis (Dahm and Molles 1990, see Figure 28).

CONCLUSIONS

Colwell's index of predictability is sensitive to the time scale of data analysis for some streams but not for others. The sensitivity varies according to previously-defined stream types (i.e., those derived in Section 1 of this report). As the time scale of analysis increases (from daily to

weekly to monthly to seasonal), some stream types become more predictable (SN, SR1, SR2, GW1, PR1, and PF), others less predictable (IF and HI) and the remainder do not change (PR2, GW2, SS, and IR). These patterns indicate the importance of regional climatic conditions and local catchment characteristics in influencing the calculation of predictability at different time scales. Thus, the use of Colwell's index to assess streamflow predictability requires some justification for the selection of a particular time scale.

For analysis of the high flow disturbance regimes across different stream types, monthly data are not capable of capturing the information available in the daily hydrograph for most streams. Only snowmelt and harsh intermittent streams are consistently above 80% in the correspondence between the timing of high monthly flows and months having the annual maximum flow.

The rank correlation between the annual mean flows and the annual peak daily flows is statistically significant for all streams types. Intermittent streams generally express higher rank correlations than perennial streams. The low absolute value of the correlation for several stream types (especially abundant eastern PR and GW streams) indicates that annual flow data are limited in their ability to confidently extract information on high flow regimes for streams where daily data are lacking.

FISH COMMUNITY STRUCTURE ALONG HYDROLOGIC GRADIENTS IN
WISCONSIN AND MINNESOTA STREAMS, AND SOME IMPLICATIONS
FOR COMMUNITY RESPONSE TO CLIMATE CHANGE

INTRODUCTION

How ecological communities will respond to rapid climate change is a
difficult question for ecologists to answer for several reasons. First, we
generally lack sufficient ecological data that can serve as a baseline against
any inferred change. Second, high natural variability in both environmental
signals and in community composition makes responses to anthropogenic climate
change difficult to document. This is particularly the case when data records
are short. Third, limited resources typically constrain our ability to gather
the types of information required to rectify the first two problems.
Moreover, suffused into each of these concerns is the inescapable issue of
"scale": At what levels of spatial, temporal, and ecological resolution must
we conduct work in order to establish bona fide patterns? Indeed, the problem
of scale has emerged in the last few years as arguably the major general
intellectual hurdle for ecologists to overcome in producing a unified and
predictive science (see O'Neill et al. 1986, Wiens 1989, Allen and Hoekstra
1992, Levin 1992).

Recent volumes on ecological responses to climate change (Regier et al.
1990, Firth and Fisher 1992, Kingsolver et al. 1992) have drawn attention to
the necessity of ecologists' "scaling-up" from their traditional local focus
to a broader regional research context, because climate change will induce
alterations at the regional scale. At this broad level of spatial resolution,
experimental studies are generally not feasible. Instead, comparative studies
that incorporate multivariate analyses are often appropriate tests of 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 (Orians 1987, Tonn et al. 1990). The application of
well-designed comparative studies is likely to provide timely information on
potential ecological responses to climate change and to suggest critical

ecological experiments (Pace 1993, cf. Cole et al. 1991). This comparative approach has been successfully applied to fish assemblages (Mahon 1984, Tonn et al. 1983, 1990, Jackson and Harvey 1989).

In community ecology, an emerging view is that the dynamic interplay among species in a local community is constrained by larger-scale environmental factors and available species pool (Ricklefs 1987, Roughgarden 1989, Menge and Olson 1990). This implies that when ecological questions are asked at regional scales, information on abiotic constraining factors and historical processes that determine the regional species pool will be crucial to understanding the regional pattern. Local processes or habitat constraints may be need to be invoked to explain residual variation in the regional pattern (Tonn 1990, Duarte 1991). For questions of variation in community structure across geographic scales, consideration both of accompanying variation in regional environmental factors and of constraints imposed by regional species pool are clearly needed. To the extent that local-regional relations for lotic communities can be established and related to climate, a potentially predictive basis can be developed for assessing ecological responses to future climate change.

In stream systems specifically, local community structure is known to be influenced by regional climatic factors. For example, temperature directly constrains performance of aquatic species and latitudinal/altitudinal gradients in thermal regimes define geographic distributions for species, such that the implications of regional warming for certain fish species can be evaluated (e.g., see Meisner 1990a). Also, energy inputs into stream ecosystems directly influence local trophic characteristics (Vannote et al. 1980), and differences among biomes in vegetation biomass and growth form result in significant variation in community structure (Corkum and Ciborowski 1988, Corkum 1989). Anthropogenic activities that alter natural thermal regimes (e.g., by impounding free-flowing rivers, Ward and Stanford 1979) or modify the energy input base (e.g., through land-use changes, Karr et al. 1986) can radically alter lotic communities, and are indicative of the kinds of changes that natural climate change likely will engender.

One climatically-influenced factor that can significantly constrain lotic community structure is the hydrologic regime. Extremes of flow (spates, droughts) and variable flow can directly influence community patterns, as has been demonstrated by a number of studies for both fish (Horwitz 1978, Coon

1987, Fausch and Bramblett 1991, Bain et al. 1988, Jowett and Duncan 1990, Meffe 1984) and invertebrates (reviewed in Resh et al. 1988, Poff and Ward 1989, Fisher and Grimm 1991). For individual fish species, spates may serve as sources of direct mortality for both juvenile (Seegrist and Gard 1972, Hanson and Waters 1974, Schlosser 1985, Harvey 1987) and adult (Toth et al. 1982, Schlosser and Toth 1984) fishes, and the timing of high flows may serve as environmental cues for spawning (John 1963, 1964, Nesler et al. 1988). Although ecologists have long intuited the importance of hydrologic regime in structuring lotic community structure, the theoretical basis for this idea was not considered until the 1980's, when stream ecologists explored the relevance of marine ecology's harsh-benign hypothesis (Peckarsky 1983) and intermediate disturbance hypothesis (Ward and Stanford 1983) to lotic communities. 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 community structure among streams is explicable in terms of hydrologic patterns, which can vary substantially over even short geographic distances (Poff and Ward 1989, Biggs et al. 1990). In the past few years, much attention has been paid to the application of Southwood's (1977, 1988) "habitat template" idea to lotic communities (Frissell et al. 1986, Minshall 1988, Poff and Ward 1990, Schlosser 1987). If habitat (and resource) availability and duration vary among locations, then differences in species assemblages across these habitats should reflect, in some measurable way, the differential abilities of species to persist and succeed under local environmental conditions. In other words, species should possess the attributes that enhance fitness given a particular template. If the template changes, due to climate change (or other factors) then one expects shifts in species composition or functional organization to occur (Carpenter et al. 1992, Grimm 1992, Poff 1992a).

Of course, hydrologic regime alone is not expected to fully explain patterns in community structure, because other important habitat features, known to have local influence, are to differing extents independent of discharge (e.g., channel morphology, substrate, gradient). The importance of these other physical habitat factors has been amply documented in the literature (e.g., Angermeier 1987, Bozek and Hubert 1992). Additionally, local heterogeneity in habitat features can create flow refugia (Sedell et al. 1990, Lancaster and Hildrew 1993) that surely disguise the signal a hydrologic

regime imposes on community structure. Nonetheless, at *regional* (among-stream) scales, there is reason to hypothesize that a substantial and ecologically interesting portion of variation in lotic community structure may reflect broad-scale hydrologic constraints (Poff 1992a), because stream discharge can serve as an integrator of catchment-scale processes (Resh et al. 1988).

If some relationships between fish community structure and hydrologic regimes can be established based on present patterns, then it should be possible to infer something about likely alterations in community structure under scenarios of climate change that modify existing hydrologic regimes in specific ways. Demonstration of such relationships would provide a basis for identifying communities (or community types) "at risk" given projected changes in climate. A similar point of view has been expressed for freshwater fish assemblages by Tonn (1990), who notes that, even in lakes, hydrologic factors can indirectly maintain local assemblage types by influencing dispersal success, extinction rates and colonization rates of species in the regional species pool.

In attempting to find fish-flow patterns, it is critical to insure that there is agreement between the scale at which the community and the environmental factors are viewed. Margalef (1968) pointed this out when he argued that large-scale patterns are best detected with coarse-grain data. Hydrologic data can be described by any number of arbitrary time scales, from instantaneous to multi-annual. The most appropriate approach is to scale the hydrologic variables to the ecological data. For ecological factors, the units of measurement can profoundly alter the perception of pattern (e.g., Allen and Starr 1982, Rahel 1990, Allen and Hoekstra 1992). 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 Skagen 1973, Allen and Starr 1982).

The method of aggregation of the ecological entities also influences perceived pattern. Two traditional approaches to viewing communities are in taxonomic terms (species identities) or in functional terms (aggregations of species into guilds of species possessing similar ecological roles and needs). When investigating environment-community patterns across zoogeographic scales, where species compositions naturally change, a functional perspective may be

necessary to provide a basis for comparison of taxonomically dissimilar communities (see Schoener 1986, 1987). Further, if environmental change adversely affects species in a community, it is likely to result in a common response among species of similar functional attributes. Such functional analyses are the basis for much of comparative ecology of both stream fish (Karr et al. 1986) and invertebrates (Vannote et al. 1980).

The primary goal of this research was to test the hypothesis that fish assemblage structure varies among unregulated streams as a function of ecologically important components of the hydrologic regime, as speculatively proposed by Poff and Ward (1989). In order to do this, we identified locations where both fish assemblage data and hydrologic data were available so that quantitative relations could be established. We wanted to compare the usefulness of taxonomic vs. functional approaches to assessing the habitat-assemblage relationships; therefore, we defined several functional attributes that we expected to be sensitive to hydrological variation and thus provide a basis for identifying hydrological-biological associations. These attributes included life history variables, trophic guild characteristics, body morphology, habitat preferences (stream size, microhabitat, and substrate), and environmental tolerance (see Methods for full description).

METHODS

Fish Data

Fish data from sites in three states (AR, MN, WI) were collected from various sources and examined for proximity to existing USGS gauging stations in those states. Fish sampling data from all three states were downloaded from the EPA's national repository of fish and water quality storage and retrieval system (STORET). Additionally, private source data were acquired from each state: the Master Fish and Waterbody file from the Wisconsin DNR (Fago 1992), a stream survey from the University of Minnesota Bell Museum of Natural History, and a collection of samples taken during a study by the Arkansas Department of Pollution Control (Giese 1987). All data are currently housed in the ERL-D Global Climate Change Information Management System.

Data collected in this fashion pose problems, including variable motivations for collection, dissimilar collection techniques and efficiency, and differential taxonomic resolution and accuracy across sites and states.

These problems are nearly impossible to rectify because the collections often date back years to decades, thus invalidating reconstruction of original field survey conditions, taxonomic accuracy, etc. Despite these limitations, archived (historical) fish collection data can be used to examine specific ecological hypotheses (e.g., see Horwitz 1978), though the strength of the interpretations must be qualified by the uncertain quality of the available data.

Locational information from the fish sample data was converted from its native state in a personal computer database to a geographic information system (GIS) coverage so it could be examined along with the USGS gauging stations. All fish collections on the gauged stream that were within a 15 km radius of the stream gauge were included as candidate sites in the dataset. For each gauged site, a map was generated that showed the local stream network and the locations of the USGS gauge and the candidate fish sampling sites. This list of potential sites was then closely examined to make sure that candidate sites were on the gauged stream and not on small tributaries or in adjacent lentic habitats. Several individual collections may have occurred within the 15 km radius of the gauge over a period of several years. Such spatial replicates were considered to be individual collections occurring at a unique location on the stream. Repeated samplings at any unique location were considered as temporal replicates for that location. For each site, the number of spatial and temporal replicates was tallied over the period for which fish data were available.

Derivation of functional measures
Life History Variables--

Life history traits are considered to be products of natural selection (Stearns 1976), and thus provide ideal functional descriptors for assessing variation in community structure along environmental selection gradients. Stream ecologists have used this approach to hypothesize that community structure should reflect variation in hydrologic selective pressures and thus show some predictable within- and among-catchment differences (e.g., Schlosser 1987, Minshall 1988, Resh et al. 1988, Poff and Ward 1989, 1990, Biggs et al. 1990, Poff 1992a). Despite the theoretical appeal of using life history variables to describe the functional composition of stream fish communities, the available compilations of appropriate life history information (Winemiller

and Rose 1992, Detenbeck et al. 1992) are inadequate for the present analysis because too many species are not included in these databases.

Body morphology measurements--

Fish ecologists have long recognized variation in body morphology of fishes from different lotic biotypes, such as riffles, runs and pools (see Nikolskii 1963, p. 75). Based on limited work, it appears that dominant morphological types in lotic fish assemblages can be influenced by hydrologic variability (Bain et al. 1988). Discussions with Dr. Paul Webb (University of Michigan) resulted in selection of two morphological ratios (Webb and Weihs 1986) that are likely to describe morphological relationships to the hydrologic environment: 1) A body shape factor defined by the ratio of total body length (TBL) to maximum body depth (MBD) describes the hydrodynamic profile of the fish (e.g., fusiform vs. bluff-body profile), which influences energetic costs of position maintenance. 2) The caudal peduncle depth factor is the ratio of minimum depth of the caudal peduncle (MDCP) and the maximum caudal fin depth (MCFD). This factor is a rough correlate for swimming ability of the fish, in that fish having a large ratio are relatively strong swimmers (e.g., thunniform fishes).

Morphological measurements for fishes were taken mainly from the Peterson Field Guide to the Freshwater Fishes (Page and Burr 1991) and the Atlas of North American Freshwater Fishes (Lee et al. 1980). Page and Burr present illustrations taken from live fishes or photographs of live or freshly killed fishes. Lee's atlas includes photographs of fishes. Measurements for three species not available from these two sources were taken from Scott and Crossman (1974) and Trautman (1981).

Four measurements were required to produce the two ratios. Total body length (TBL) was the overall length of the pictured fish, including all of the caudal fin and all of the mouth. This was the maximum length of the picture on the page. Maximum depth of body (MDB) was the maximum height of the body only. Fins, stickles, and other appendages were not included in this measurement. Minimum depth of the caudal peduncle (MDCP) was the smallest point of the caudal peduncle, not including any fins. Maximum Caudal Fin Depth (MCFD) was the maximum height of the caudal fin, regardless of shape.

All measurements were taken using a dial caliper graded to 0.254 mm (= 0.01 in). In some cases, an estimate was made to the nearest 0.127 mm.

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Because the ratios are dimensionless, the units of measurement for the four variables needed only to be consistent for a particular fish. The photographs from Lee's atlas may have introduced some inaccuracy in the cases where the caudal fin was slightly compressed from top to bottom, where photographs were too light in the caudal fin section to allow accurate measurement, or where photographs were trimmed too much for inclusion in the atlas. (Some photos had noticeable trim lines, with extra portions of the background showing, and some had no background showing, which could mean a portion of the fish was trimmed from the photo.)

Trophic Guild--

A number of authors have proposed trophic or feeding categories for stream fishes (Horwitz 1978, Moyle and Li 1979, Grossman et al. 1982, Schlosser 1982). K.R. Allen (1969) offered a simple classification for North American stream fishes: most are invertivores, some become piscivorous later in their life cycle, and a few are herbivorous. While broadly correct, this scheme fails to capture significant additional variation in feeding habits, primarily in terms of where and how fishes capture their food (Table 11). Some invertivores feed primarily from the benthos, others from the water column and surface, and still others appear to be generalists. There also is considerable variation in the amount of plant matter consumed. 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. Planktivore and parasitic categories are also represented in our data set. Fish were assigned to trophic categories based on descriptions in Lee et al. (1980) and Scott and Crossman (1974).

Habitat Classification--

Habitat preferences were established from descriptions of fish habitat included in references describing stream fishes from North America of the midwestern region (Becker 1983, Lee et al. 1980, Scott and Crossman 1974, Trautman 1981). Although there is a large amount of literature on fish habitat utilization, to our knowledge there are no generally accepted habitat categories parallel to trophic categories. We first examined habitat descriptions from standard references, and then by trial and error developed

categories that appeared to allow useful separation of species into major

habitat categories in terms of current, substrate, and stream size. For each

TABLE 11. FUNCTIONAL MEASURES OF FISH SPECIES. SCORES FOR EACH
SPECIES GIVEN IN APPENDIX D

Body Morphology   (continuous)
    1. Swimming Factor
    2. Shape Factor

Trophic Guild   (categorical)
    1. Herbivore-detritivore
    2. Omnivore
    3. General Invertivore
    4. Surface/Water column Invertivore
    5. Benthic Invertivore
    6. Piscivore[a]
    7. Planktivore
    8. Parasite

Habitat Classification

Flow Habitat   (categorical)
    1. Fast
    2. Moderate
    3. Slow-none
    4. Generalist

Substrate Preference   (categorical)
    1. Rubble (rocky, gravel)
    2. Sand
    3. Silt
    4. Generalist

Stream Size   (categorical)
    1. Small[b]
    2. Medium-Large[c]
    3. Small-Large[d]
    4. Lake

Silt Tolerance   (categorical)
    1. Intolerant
    2. Moderately Tolerant
    3. Tolerant

[a] includes fishes feeding on large invertebrates such as crayfish
[b] fishes of small streams and headwaters, and of both small and   medium streams
[c] found in medium-sized streams and large rivers
[d] reported in small, medium, and large streams and rivers

habitat category, subcategories were established (Table 11). All 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. In a number of instances it was necessary to use a "generalist" category.

Environmental Tolerance--

Tolerance refers to tolerance of silt and is based on expert opinion. Species in our database that were not classified into tolerance categories by the Ohio EPA (1979) were given tolerance scores based on the other references cited above and on expert opinion (see below). Three tolerance categories were established (Table 11).

Confidence--

Our confidence in the accuracy with which fish species are placed into trophic, habitat, and tolerance categories is variable. Many species inhabited a range of categories, and information varied in its completeness, sometimes appearing inconsistent. After developing the categories of Table 11 and assigning each species a code, the results were submitted to expert fish biologists for evaluation (G.R. Smith, Museum of Zoology, University of Michigan, Paul Seelbach, Institute for Fisheries Research, Michigan Department of Natural Resources). However, it is not yet possible to designate all species unambiguously into appropriate categories. When sufficient information was available and all sources agreed, a code of 3 (high confidence) was given. When little information was available, when sources conflicted, or when the biological information did not allow a species to be well described by a single category, a confidence code of 1 or 2 was assigned. Species' scores for the attributes listed in Table 11 are given in Appendix D (and also provided on diskette).

Hydrologic Data

Variables for each gauged site were derived from the long-term hydrologic dataset and named in Section 1. The following variables were used: DAYCV, DAYPRED, FLDFREQ, FLDPRED, FLDFREE, BFI, ZERODAY, LOWPRED, LOWFREE. These variables represent long-term averages over variable periods of record

TABLE 12. SAMPLING CHARACTERISITCS OF 34 WIMN SITES. FOR EACH SITE, THE NUMBER OF UNIQUE SPECIES COMBINED ACROSS ALL COLLECTIONS SINCE 1960 ARE GIVEN, AS ARE THE TOTAL NUMBER OF COLLECTIONS AND THE PERIOD OF AVAILABLE HYDROLOGIC DATA

Gauge #	state	number species	number samples	streamflow record
4063700	WI	22	4	1964-1986
4078500	WI	41	12	1929-1985
4080000	WI	44	6	1929-1970
4081000	WI	51	17	1929-1963
4085200	WI	25	5	1967-1986
4086500	WI	35	32	1931-1970
5069000	MN	21	21	1948-1983
5293000	MN	25	3	1940-1985
5300000	MN	34	9	1934-1985
5311400	MN	25	5	1961-1981
5313500	MN	27	3	1940-1985
5315000	MN	21	4	1941-1985
5316500	MN	32	5	1936-1985
5317000	MN	29	2	1939-1985
5332500	WI	31	6	1929-1970
5333500	WI	24	2	1929-1981
5367500	WI	36	10	1929-1961
5368000	WI	34	5	1951-1986
5374000	MN	23	3	1931-1980
5379500	WI	54	40	1935-1986
5381000	WI	24	5	1929-1986
5383000	WI	51	21	1929-1970
5394500	WI	24	4	1940-1986
5397500	WI	21	4	1940-1986
5406500	WI	32	11	1955-1986
5413500	WI	35	7	1935-1986
5414000	WI	45	16	1935-1986
5415000	WI	26	6	1940-1986
5423000	WI	31	16	1950-1970
5423500	WI	22	14	1949-1969
5424000	WI	34	19	1950-1970
5432500	WI	39	9	1940-1986
5433000	WI	36	9	1940-1986
5543830	WI	34	8	1964-1986

at gauged locations (see Table 12). (The derivation of these variables is provided in detail in Section 1 of this report). All gauged stream sites in the database within within 15 km of a fish sampling station were screened for unacceptable sources of hydrologic disturbance (impoundment, hydroelectric facilities, irrigation withdrawal, etc.). The list of candidate sites was then cross-checked against the two independently-derived datasets listing stream gauges that have been stable over the entire period of record (Wallis

et al. 1991, Slack and Landwehr 1992). Some sites did not appear on these lists. Telephone conversations with U.S. Geological Survey personnel responsible for original screening of sites for inclusion in the Slack and Landwehr (1992) list confirmed that the unmatched sites could have been included in the original listings, but typically were not because the gauges had been discontinued several years ago. Thus, all sites used in the analysis have acceptably unmodified hydrologic regimes.

Data Analysis

Fish Data Matrices--

Several decisions had to be made to determine which data were suitable for inclusion. First, we excluded all fish samples collected prior to 1960, in order to keep the fish data relatively contemporary. A total of 24, 33 and 43 potential sites with fish data were identified for AR, MN, and WI, respectively. The intensity of collections varied markedly among sites, as did the number of species collected per site. The relationships between species number and sampling intensity are shown for all the AR, MN, and WI sites in Figure 29. In order to diminish the likelihood that any observed pattern in assemblage structure simply reflected sampling intensity, a decision was made to include only sites with $\geq$ 20 species present across all spatial-temporal replicates, regardless of how many collections were made (Table 12). We considered this an acceptable tradeoff between minimizing artifacts caused by sampling intensity and retaining enough sites in the database to perform a valid analysis.

All data from AR were excluded from further analysis because too few sites had sufficient species richness. Fish diversity in AR is very high (Robison and Buchanan 1988), and the paucity of species in the EPA database indicates a problem with the original data source in terms of sampling efficiency and/or archival techniques. In WI and MN, 25 and 9 sites, respectively, contained $\geq$ 20 species and were acceptable hydrologically. To increase sample size, sites from these two states were combined into a "regional" dataset (hereafter referred to as WIMN) containing 34 locations (Figure 30). This is reasonable since the two states are adjacent and share common drainages.

A linear relationship between species richness and sampling intensity persisted when the 34 WIMN sites were considered together (Figure 31), though

there was much scatter about the line of central tendency. This relationship indicates that any observed hydrological-ecological pattern must be carefully examined for possible confounding with sampling intensity. Another potentially confounding factor is stream size, which can influence taxonomic composition and species richness. Neither the entire WI and MN datasets (Figure 32) nor the 34 WIMN sites (Figure 33) showed any systematic relationship between species richness and catchment area (a strong correlate of stream size).

Data from the WIMN sites varied in terms of its information content. Almost half of the retained sites contained only presence/absence (+/-) data. Thus, it was necessary to collapse all abundance data from sites into binary data. Given the aforementioned problems with the original data, an analysis based solely on +/- data is prudent.

Community Structure: Taxonomic Organization--

The data for this analysis consisted of a 34 site by 106 species matrix. The 106 species represented the sum of unique species present across all sites at all times (Table 13). In the original dataset, 12 "species" were identified as unknowns and eliminated from the analysis. Each entry in the matrix was either a "1" (species present at site) or an "0" (species absent). There were two objectives of this taxonomic analysis. First, we wished to determine similarity of sites based on species composition and use multivariate techniques to explore any patterns that related to among-site hydrologic variables. To do this we used a variety of classification and ordination techniques (described below). Second, we wished to test the hypothesis that taxonomic composition across sites was explainable in terms of hydrologic variables. To do this we used discriminant analysis.

Ordination and Classification--A variety of multivariate techniques can be used to explore patterns in ecological communities (see Gauch 1982, Ludwig and Reynolds 1988). Two frequently used approaches are ordination and classification. Ordination summarizes community data by reducing a complex multi-dimensional dataset to a low-dimensional (typically 1-3) space in which similar samples (sites) fall closely together along species' gradients and dissimilar samples are well separated (Gauch 1982). The positions of sites in

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species space can then be compared with environmental information for the sites to see if differences in community composition correlate with the

TABLE 13. LIST OF UNIQUE SPECIES RECORDED ACROSS ALL 34 WIMN SITES (UPPER PANEL) AND NUMBER OF SITES AT WHICH EACH SPECIES OCCURRED (LOWER PANEL). NAMES FOR SPECIES ABBREVIATIONS ARE GIVEN IN TABLE 16

BMS	LND	SDS	TRP	CSH	JND	WTS	SPS	CRC	FHM	BSD	BKB	SCT
GLR	ROS	CCF	NOP	SAR	WAE	FWD	SHR	SRL	BLM	HHC	BND	EMS
LKC	OSS	BLC	BLG	TPM	YEP	BST	SLR	CAP	SPO	SHD	GSF	BIB
IOD	WHC	QBS	FTD	RBD	BDD	NHS	SMB	RKB	BHM	RVS	BNT	GIS
BNS	WHB	SNG	LNG	RCS	SAB	SPC	SKM	LGP	NRD	MTS	PRD	FND
RBT	GOS	CNM	BKT	SIL	BUB	LKS	LSR	PMK	LMB	MMS	WSD	YEB
RVD	RSD	SRD	BTM	RES	GRR	SRS	GLD	CHL	RRH	MUE	BKS	FCF
WDS	ABL	MOE	MDD	HFS	SLC	BOF	AME	MSM	GOE	OZM	BLT	BRB
LCS	GPK											

20	16	21	2	34	30	33	23	33	24	23	18	22
19	14	10	24	8	18	6	21	8	30	26	18	14
5	9	12	17	8	14	11	18	24	7	11	18	5
3	5	10	17	9	13	16	20	15	4	6	13	4
6	6	2	3	5	2	1	8	10	5	6	4	1
9	8	12	4	4	8	1	10	11	11	5	2	9
1	1	9	1	2	3	1	2	5	1	1	4	3
1	3	3	1	3	1	2	1	1	1	1	1	1
1	1											

environmental data. Of the many ordination techniques available, detrended correspondence analysis (DCA, Hill 1979a) has many favorable characteristics which combine to make it a powerful technique for examining community relations (Gauch 1982). The principal strength of DCA is that it imposes the stringent condition that second and higher order axes have no systematic relations of any kind to lower axes, unlike all other ordination techniques (e.g., principal components analysis, polar ordination, canonical correlation analysis), which simply constrain higher axes to be linearly uncorrelated (orthogonal) with lower axes (Gauch 1982). DCA has been used extensively in the ecological literature, including in the analysis of lotic community structure for both abundance and binary data (Ormerod 1987, Ormerod and Edwards 1987, Moss et al. 1987, Poff et al. 1990, Rahel and Hubert 1991, Boulton et al. 1992).

Classification is a method of placing ecological entities (species, sites) into classes or groups. In this paper, sites having similar taxonomic composition would group together while dissimilar sites would not, based on a measures of multivariate distance in overall species space. Hierarchical clustering routines produce dendrograms that can be viewed at various levels of resolution to identify various numbers of classes or groups. Hierarchical classification is best suited to small datasets (n < 100) whose hierarchical structure can be visually comprehended (Gauch 1982). Of the many techniques available for classification of ecological community data, two-way indicator species analysis (TWINSPAN, Hill 1979b) has the unique property of "deliberately arrang[ing] the two clusters at each node in the way that results in placing the most similar samples together in the dendrogram's sample sequence," and thus facilitating interpretation (Gauch 1982, p. 201). TWINSPAN has been widely used as a classification tool for ecological communities, including those in streams (Wright et al. 1983, Ormerod 1987, Ormerod and Edwards 1987, Moss et al. 1987, Poff et al. 1990). It is also appropriate for binary data and is often used as a complement to DCA.

Discriminant Analyses--*Canonical discriminant analysis* (CDA) is a multivariate technique that derives canonical variables (linear combinations of quantitative variables) that have the highest possible multiple correlation with previously-defined classes (SAS 1988). In this paper, the classes are groups of ecologically-similar sites and the quantitative variables are the 9 hydrologic variables for each of the 34 WIMN sites. The maximum number of canonical variables that can be derived equals the number of previously-defined groups, minus one. CDA is a three step process. First, classes (groups of sites) are defined in ecological terms that are independent of the hydrologic variables. Second, linear combinations of the hydrologic variables are derived that best describe the separation of the classes. Third, the hypothesis that class means are the same in terms of the hydrologic variables is tested, as is the hypothesis that the correlation between the canonical variables and the ecological groups is equal to zero. Rejection of these hypotheses indicates that the hydrologic variables can discriminate among the ecologically-defined groups. Interpretation is based on examining the correlations between the original hydrologic variables and the canonical variables to see which hydrologic variables are most important in explaining

the discrimination among the classes. CDA requires the assumption of multivariate normality of the (hydrologic) variables to be examined. A good rule of thumb is that if all variables show univariate normality, multivariate normality is a reasonable assumption. Visual inspection of the 9 hydrologic variables indicated that all but ZERODAY (which has many zero values) were approximately normally distributed. CDA is essentially a dimension reduction technique useful in exploring ecological-environmental relations, and it has been used extensively in the ecological literature, including in studies of fish ecology (e.g., Hawkes et al. 1986, Bozek and Hubert 1992, Nelson et al. 1992).

Discriminant function analysis (DFA) is another, related multivariate technique that classifies observations on the basis of one or more quantitative variables into two or more known (previously defined) groups (Johnson and Wichern 1982, SAS 1988). DFA also produces a quantitative function relating group affiliation (based on ecological similarity) to environmental variables, and it has two major strengths. First, it can be used to determine the classification error rate for the original observations. If the quantitative function derived from the hydrologic variables can completely discriminate among the previously-defined ecological groups, then the DFA is 100% effective in predicting ecological class from environmental data. Second, the quantitative function can be used to predict the membership of new sites into ecological groups based only on environmental data (e.g., see Marchant et al. 1984, Bozek and Hubert 1992, Norris and Georges 1993). DFA also requires the assumption of multivariate normality of the (hydrologic) variables to be examined. Two analyses were made with DFA: a non-parametric test including ZERODAY and a parametric test excluding ZERODAY from the analysis (see SAS 1988, p. 360 ff.).

Three steps were required to test the hypothesis that taxonomic composition of fish assemblages varied with hydrologic factors for the 34 WIMN sites. First, assemblage similarity among sites was calculated using the Jaccard coefficient, a measure specifically designed for binary data (Dyer 1978). Second, sites were classified into 2-3 groups based on similarity using a hierarchical clustering routine (Ward's minimum variance method) on SAS. A separate analysis was performed where groups were defined by the TWINSPAN classification. Third, hydrologic factors for each site were used as

quantitative variables to try to discriminate (using CDA and DFA) among the previously-defined ecological groups.

Community Structure: Functional Organization--

The data for this analysis consisted initially of a 34 site x 25 functional attribute matrix. The structure of this matrix requires some detailed explanation. As described above, for each unique species in the overall dataset, functional information was available for 25 individual categories and subcategories. The two morphology categories contained continuous data, whereas the 5 trophic, habitat, and tolerance categories (total of 23 subcategories) contained only categorical data (see Table 11). For each site (row in the matrix), the following procedure was applied: for the continuous (morphological) variables, the *average* value for all species present was calculated and entered, whereas for the categorical attributes, the *proportion* of all species falling into subcategories within a major category was determined. For example, if 40 species were present at Site Z, the value entered in the matrix for the first morphology attribute was calculated by averaging the 40 species' values for that attribute. As an example of the categorical calculation, the trophic category contained 8 subcategories. If 10 of the hypothetical 40 species present at Site Z 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 Site Z. The remaining six trophic subcategory proportions were similarly determined, so that within the trophic attribute category, all subcategory scores would sum to 1.00 (or slightly less in some cases where a species with an undefined attribute occurred). This step was repeated for each of the five major categorical attributes. After the matrix was constructed, the variables were standardized to mean of 0 and standard deviation of 1 and a correlation matrix was derived that described the similarity among sites in the functional attribute space (i.e., sites with functionally similar fish assemblages would be highly correlated). This correlation matrix (dimension 34 x 34) was then used as input into a hierarchical cluster analysis (Ward's method) using SAS and 2-3 ecologically-similar groups were specified and defined. The groups were then used in DFA and CDA to test the null hypothesis that ecologically-similar assemblages (defined in functional terms) cannot be discriminated by the hydrologic variables.

Ward's method defines distance between two clusters as the "ANOVA sum of squares added up over all the [functional] variables" (SAS 1988, p. 296). The procedure assumes a multivariate normality and is sensitive to outliers. Visual inspection of normal probability plots of the 25 functional attribute variables showed that almost all were approximately normally distributed. Exceptions included only those variables that were not represented at all sites (e.g., parasitic trophic category).

For the major functional attributes (Table 11), means and standard errors for the groups identified by cluster analysis were plotted. Oneway analysis of variance (SAS 1988) was used for each functional category to test the hypothesis of no statistically significant difference among groups. To meet parametric assumptions, morphological data were log-transformed and other, proportional functional data were arcsin-transformed prior to performing ANOVA (Steel and Torrie 1980). Differences among groups were tested with the Student-Newman-Keuls multiple comparison test, with $\alpha = 0.05$. As a check against possible violations of the parametric assumption of normality, non-parametric one-way analysis of variance was also performed using the Wilcoxon (2-sample) and Kruskal-Wallis (3-sample) tests (Steel and Torrie 1980, SAS 1988).

RESULTS

Hydrologic Variables

The long-term averages for the various hydrologic variables for each of the 34 WIMN sites are given in Table 14. Of the 34 sites, 21 were cross-referenced by Slack and Landwehr (1992) and Wallis et al. (1991) and were classified according to the methods presented in Section 1 of this report. Six of the 10 classification types present in the entire U.S. were represented by the 21 streams in WI and MN. Hydrologic characteristics for the 13 unclassified sites were visually inspected and an assignment was made to one of the 10 groups defined in Section 1 (in parentheses in Table 14). Almost all streams are perennial, with the greatest proportions represented by superstable (SS, n = 12), mesic groundwater (GW, n = 6), and perennial runoff (PR, n = 12) streams. Intermittent runoff (IR) streams occur twice, while snow+rain (SR) and snowmelt (SN) streams were represented by one site each.

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The correlations among the hydrologic variables across the 34 WIMN sites are given in Table 15.

Fish Species Occurrences

A total of 106 unique fish species were represented across the 34 WIMN sites (Table 16). Of these 106 species, only one (common shiner) occurred at all 34 sites, although 4 others were recorded at ≥ 30 sites (see Table 22, "total sites" column). 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 WIMN sites (see Table 22).

Fish Taxonomic Relationships to Hydrologic Factors

The TWINSPAN analysis resulted in the hierarchical dendrogram shown in Figure 34. The number of groups of sites specified in the dendrogram depends on the level at which the user defines a division. At 1 level of division, 2 groups resulted; at 2 levels of division, 4 groups of sites resulted; and , at 3 levels of division, 8 groups of sites were generated. Individual "indicator" species that have high relative weighting in splitting a large group of sites into two smaller groups are shown at each branch in the dendrogram (Figure 34). For example, at the first division, largescale stoneroller (LSR) is an "indicator" species for groups 1 and 2, while the sand shiner (SDS), bigmouth shiner (BMS), common stoneroller (SRL), and plains carpsucker (= quillback) (QBS) are "indicators" for groups 3 and 4. Indicator species can occur at more than one branch point, as evidenced by SRL, which occurs twice in the 2-level division. At the third division, groups 1 and 2 are distinguished largely on the basis of northern hogsucker (NHS), while groups 3 and 4 are divided according to the proportional presence of SRL and brown trout (BRT).

The geographic distribution of the sites comprising the four TWINSPAN groups is shown in Figure 35. There is clear regional clustering of the sites when clustered according to taxonomic affiliation, and these patterns probably reflect zoogeography. TWIN 1 sites tend to occur along the Lake Michigan shore of Wisconsin; TWIN 2 sites are located in northern, interior Wisconsin; and, TWIN 4 sites are restricted to southwestern Wisconsin. TWIN 3 sites are almost entirely restricted to Minnesota, with the exception of one SW

TABLE 14. SUMMARY OF HYDROLOGIC VARIABLES FOR 34 WIMN SITES. CLASS REFERS TO STREAM CLASSIFICATION (FROM SECTION 1, THIS REPORT). INFERRED CLASSIFICATIONS FOR PREVIOUSLY UNCLASSIFIED SITES ARE ENCLOSED IN PARENTHESES. GROUP REFERS TO ECOLOGICAL GROUP (AS IDENTIFIED WITH CANONOICAL DISCRIMINANT ANALYSIS -- SEE TEXT), WHERE 1 = "VARIABLE", 2 = "MODERATELY STABLE", AND 3 = "VERY STABLE". TWIN REFERS TO THE 2-LEVEL TWINSPAN CLASSIFICATION FOR EACH SITE (REFER TO FIG. 34).

Gauge	State	Class	Group	Twin	DAYCV	DAY-PRED	FLD-FREQ	FLD-PRED	FLD-FREE	BFI	ZERO-DAY	LOW-PRED	LOW-FREE
4063700	WI	SR	1	1	103.55	73.47	0.43	0.75	0.45	0.24	0.0	0.63	0.37
4078500	WI	GW	3	2	102.71	73.71	0.70	0.68	0.35	0.25	0.0	0.56	0.44
4080000	WI	(GW)	2	2	95.82	75.98	0.62	0.72	0.24	0.34	0.0	0.48	0.32
4081000	WI	(SS)	1	2	44.45	74.71	0.57	0.79	0.23	0.55	0.0	0.34	0.27
4085200	WI	PR	2	1	211.14	58.52	0.50	0.73	0.29	0.14	0.0	0.57	0.53
4086500	WI	(PR)	1	1	186.68	45.73	0.88	0.64	0.37	0.08	0.0	0.39	0.29
5069000	MN	SN	2	3	212.20	55.94	0.58	0.81	0.69	0.10	0.0	0.50	0.45
5293000	MN	PR	1	3	257.11	28.66	0.76	0.61	0.50	0.02	0.01	0.60	0.35
5300000	MN	IR	1	3	236.15	23.99	0.87	0.79	0.59	0.01	0.08	0.48	0.30
5311400	MN	(IR)	1	3	321.88	24.99	0.67	0.62	0.54	0.00	0.2	0.48	0.21
5313500	MN	PR	2	3	231.90	33.99	0.70	0.67	0.59	0.02	0.0	0.50	0.41
5315000	MN	(PR)	1	3	204.08	28.44	0.78	0.75	0.61	0.02	0.02	0.54	0.39
5316500	MN	PR	1	3	201.53	32.49	1.06	0.56	0.28	0.02	0.0	0.39	0.38
5317000	MN	PR	1	3	192.94	45.33	0.89	0.63	0.32	0.05	0.0	0.29	0.16
5332500	WI	(SS)	3	2	39.91	78.59	0.74	0.58	0.41	0.51	0.0	0.47	0.35
5333500	WI	SS	3	2	54.18	78.47	0.60	0.61	0.54	0.53	0.0	0.35	0.21
5367500	WI	(SS)	3	2	84.89	74.27	0.73	0.73	0.44	0.37	0.0	0.53	0.33
5368000	WI	GW	3	2	103.88	73.96	0.58	0.58	0.22	0.48	0.0	0.57	0.39
5374000	MN	PR	2	3	178.29	70.65	0.74	0.53	0.42	0.17	0.0	0.58	0.51
5379500	WI	SS	1	4	93.53	74.05	0.60	0.71	0.24	0.46	0.0	0.43	0.39
5381000	WI	PR	3	2	230.84	53.12	0.76	0.52	0.38	0.04	0.0	0.55	0.35
5383000	WI	(SS)	1	4	60.40	74.12	0.60	0.48	0.31	0.48	0.0	0.47	0.18
5394500	WI	SS	3	2	97.12	75.93	0.68	0.60	0.42	0.38	0.0	0.38	0.35
5397500	WI	SS	3	2	146.29	71.69	0.60	0.71	0.44	0.22	0.0	0.40	0.27
5406500	WI	(SS)	2	4	68.09	69.82	0.66	0.54	0.28	0.60	0.0	0.36	0.28
5413500	WI	GW	2	4	174.55	68.43	0.85	0.55	0.14	0.41	0.0	0.41	0.23
5414000	WI	GW	2	4	161.39	67.48	0.77	0.40	0.17	0.37	0.0	0.62	0.34
5415000	WI	SS	1	4	191.44	62.37	0.66	0.46	0.29	0.34	0.0	0.30	0.15
5423000	WI	(PR)	1	1	196.57	26.90	0.95	0.65	0.35	0.04	0.02	0.50	0.51
5423500	WI	(PR)	1	1	205.16	27.19	0.86	0.53	0.23	0.02	0.01	0.50	0.46
5424000	WI	(PR)	1	1	167.96	46.78	0.81	0.55	0.19	0.05	0.0	0.80	0.57
5432500	WI	SS	2	3	155.34	67.73	0.60	0.64	0.42	0.34	0.0	0.42	0.23
5433000	WI	SS	2	4	121.09	69.83	0.70	0.60	0.30	0.47	0.0	0.54	0.19
5543830	WI	(GW)	1	1	112.63	55.23	0.57	0.64	0.37	0.13	0.0	0.71	0.59

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TABLE 15. PEARSON CORRELATION MATRIX FOR HYDROLOGIC VARIABLES ACROSS 34 WIMN SITES. THE R-VALUES THAT ARE SIGNIFICANT AT P < 0.05 USING A BONFERRONI TEST ARE INDICATED BY BOLDFACE AND "*"

	AREA	DAYAVE	DAYCV	DAYPRED	FLDFREQ	FLDPRED	FLDFREE	BFI	ZERODAY	LOWPRED	LOWFREE
AREA	1.000										
DAYAVE	**0.784***	1.000									
DAYCV	-0.087	-0.452	1.000								
DAYPRED	0.098	0.490	**-0.822***	1.000							
FLDFREQ	0.149	-0.165	0.412	**-0.596***	1.000						
FLDPRED	0.120	-0.015	-0.013	-0.074	-0.295	1.000					
FLDFREE	0.305	0.107	0.328	-0.327	-0.118	0.496	1.000				
BFI	0.005	0.395	**-0.843***	**0.853***	-0.461	-0.168	-0.386	1.000			
ZERODAY	-0.069	-0.199	0.521	-0.478	0.078	0.116	0.346	-0.331	1.000		
LOWPRED	-0.224	-0.176	0.138	-0.133	-0.117	-0.014	-0.007	-0.316	0.001	1.000	
LOWFREE	-0.187	-0.201	0.120	-0.220	0.037	0.169	0.001	-0.414	-0.180	**0.700***	1.000

TABLE 16. LISTING OF 106 TOTAL UNIQUE SPECIES COLLECTED ACROSS ALL 34 WIMN SITES SINCE 1960

Abbrev.	Common Name	Genus	species
ABL	AMERICAN BROOKLAMPREY	Lamptera	lamottei
AME	AMERICAN EEL	Anguilla	rostrata
BCS	BLACKCHIN SHINER	Notropis	heterodon
BDD	BANDED DARTER	Etheostoma	zonale
BHM	BULLHEAD MINNOW	Pimephales	vigilax
BIB	BIGMOUTH BUFFALO	Ictiobus	cyprinellus
BKB	BLACK BULLHEAD	Ictalurus	melas
BKF	BANDED KILLIFISH	Fundulus	diaphanus
BKS	BROOK SILVERSIDE	Labidesthes	sicculus
BKT	BROOK TROUT	Salvelinus	fontinalis
BLC	BLACK CRAPPIE	Pomoxis	nigromaculatus
BLG	BLUEGILL	Lepomis	macrochirus
BLM	BLUNTNOSE MINNOW	Pimephales	notatus
BLT	BLOATER	Coregonus	hoyi
BMS	BIGMOUTH SHINER	Notropis	dorsalis
BND	BLACKNOSE DACE	Rhinichthys	atratulus
BNS	BLACKNOSE SHINER	Notropis	heterolepis
BNT	BROWN TROUT	Salmo	trutta
BOF	BOWFIN	Amia	calva
BRB	BROWN BULLHEAD	Ictalurus	nebulosus
BSD	BLACKSIDE DARTER	Percina	maculata
BST	BROOK STICKLEBACK	Culaea	inconstans
BTM	BLACKSTRIPE TOPMINNOW	Fundulus	notatus
BUB	BURBOT (LING)	Lota	lota
CAP	CARP	Cyprinus	carpio
CCF	CHANNEL CATFISH	Ictalurus	punctatus
CHL	CHESTNUT LAMPREY	Icthyomyzon	castaneus
CNM	CENTRAL MUDMINNOW	Umbra	limi
CRC	CREEK CHUB	Semotilus	atromaculatus
CSH	COMMON SHINER	Notropis	cornutus
EMS	EMERALD SHINER	Notropis	atherinoides
FCF	FLATHEAD CATFISH (YELLOW)	Pylodictis	olivaris
FHM	FATHEAD MINNOW	Pimephales	promelas
FND	FINESCALE DACE	Phoxinus	neogaeus
FTD	FANTAIL DARTER	Etheostoma	flabellare
FWD	FRESHWATER DRUM	Aplodinotus	grunniens
GIS	GIZZARD SHAD	Dorosoma	cepedianum
GLD	GILT DARTER	Percina	evides
GLR	GOLDEN REDHORSE	Moxostoma	erythrurum
GOS	GOLDEN SHINER	Notemigonus	crysoleucas
GOE	GOLDEYE	Hiodon	alosoides
GPK	GRASS PICKEREL	Esox	americanus
GRR	GREATER REDHORSE	Moxostoma	valenciennesi
GSF	GREEN SUNFISH	Lepomis	cyanellus
HFS	HIGHFIN CARPSUCKER	Carpiodes	velifer
HHC	HORNYHEAD CHUB	Nocomis	biguttatus
IOD	IOWA DARTER	Etheostoma	exile
JND	JOHNNY DARTER	Etheostoma	nigrum
LCS	LAKE CHUBSUCKER	Erimyzon	sucetta
LGP	LOGPERCH	Percina	caprodes
LKC	LAKE CHUB	Couesius	plumbeus
LKS	LAKE STURGEON	Acipenser	fulvescens

LMB	LARGEMOUTH BASS	Micropterus	salmoides
LND	LONGNOSE DACE	Rhinichthys	cataractae
LNG	LONGNOSE GAR	Lepisosteus	osseus
LSR	LARGESCALE STONEROLLER	Campostoma	oligolepis
MDD	MUD DARTER	Etheostoma	aspirgene
MMS	MIMIC SHINER	Notropis	volucellus
MOE	MOONEYE	Hiodon	tergisus
MSM	MISSISSIPPI SILVERY MINNOW	Hybognathus	nuchalis
MTS	MOTTLED SCULPIN	Cottus	bairdi
MUE	MUSKELLUNGE	Esox	masquinongy
NHS	NORTHERN HOGSUCKER	Hypentelium	nigricans
NOP	NORTHERN PIKE	Esox	lucius
NRD	NORTHERN REDBELLY DACE	Phoxinus	eos
OSS	ORANGE SPOTTED SUNFISH	Lepomis	humilis
OZM	OZARK MINNOW	Dionda	nubila
PMK	PUMPKINSEED	Lepomis	gibbosus
PRD	PEARL DACE	Semotilus	margarita
QBS	PLAINS CARPCUCKER (QUILLBACK)	Carpiodes	cyprinus
RBT	RAINBOW TROUT	Oncorhynchus	mykiss
RBD	RAINBOW DARTER	Etheostoma	caeruleum
RCS	RIVER CARPSUCKER	Carpiodes	carpio
RES	REDFIN SHINER	Notropis	umbratilis
RKB	ROCK BASS	Ambloplites	rupestris
ROS	ROSYFACE SHINER	Notropis	rubellus
RRH	RIVER REDHORSE	Moxostoma	carinatum
RSD	REDSIDE DACE	Clinostoma	elongatus
RVS	RIVER SHINER	Notropis	blennius
RVD	RIVER DARTER	Percina	shumardi
SAB	SMALLMOUTH BUFFALO	Ictiobus	bubalus
SAR	SAUGER	Stizostedion	canadense
SCT	STONECAT	Noturus	flavus
SDS	SAND SHINER	Notropis	stramineus
SHD	SLENDERHEAD DARTER	Percina	phoxocephala
SIL	SILVER LAMPREY	Ichthyomyzon	unicuspis
SHR	SHORTHEAD REDHORSE	Moxostoma	macrolepidotum
SKM	SUCKERMOUTH MINNOW	Phenacobius	mirabilis
SLC	SILVER CHUB	Hybopsis	storeriana
SLR	SILVER REDHORSE	Moxostoma	anisurum
SMB	SMALLMOUTH BASS	Micropterus	dolomieui
SNG	SHORTNOSE GAR	Lepisosteus	platostomus
SPO	SPOTTAIL SHINER	Notropis	hudsonius
SPS	SPOTFIN SHINER	Notropis	spilopterus
SPC	SPECKLED CHUB	Hybopsis	aestivalis
SRD	SOUTHERN REDBELLY DACE	Phoxinus	erythrogaster
SRL	COMMON (CENTRAL) STONEROLLER	Campostoma	anomalum
SRS	STRIPED SHINER	Notropis	chrysocephalus
TPM	TADPOLE MADTOM	Noturus	gyrinus
TRP	TROUT PERCH	Percopsis	omiscomaycus
WAE	WALLEYE	Stizostedion	vitreum
WDS	WEED SHINER	Notropis	texanus
WHB	WHITE BASS	Morone	chrysops
WHC	WHITE CRAPPIE	Pomoxis	annularis
WSD	WESTERN SAND DARTER	Ammocrypta	clara
WTS	WHITE SUCKER	Catostomus	commersoni
YEB	YELLOW BULLHEAD	Ictalurus	natalis
YEP	YELLOW PERCH	Perca	flavescens

Wisconsin stream. Lumping together TWIN 1+2 and TWIN 3+4 into only 2 large

TWINSPAN groups (see Figure 34) results in the WIMN 34 sites falling into a

cluster of eastern and northern-interior Wisconsin streams on the one hand

(all circles in Figure 34), and a cluster of western Wisconsin and Minnesota

streams on the other (all squares in Figure 34).

The DCA of the 34 sites based on the binary taxonomic dataset produced

four ordination axes, the first two of which explained 66% of the total

reported variance in species space (Table 17). The position of the 34 sites

with respect to the first three DCA axes is shown in Figure 36, which shows

that there is wide separation in species space among the groups of

taxonomically-similar sites (as classified by TWINSPAN) on the first three DCA

axes. DCA1 separates TWINSPAN groups 1 and 2 from groups 3 and 4, while DCA2

further separates groups 1 and 2 (Figure 36a). Groups 3 and 4 are clearly

separated along DCA3 (Figure 36b). The ordination of the individual

species on the first 2 DCA axes can be used to illustrate species

gradients across the sites (Figure 37). DCA1 indicates a gradient from

TABLE 17. CORRELATIONS BETWEEN DCA AXES AND 2 STATIC BASIN
DESCRIPTOR AND 9 HYDROLOGIC VARIABLES FOR 34 SITES BASED ON
BINARY DATA. (+ = P $\leq$ 0.10, * = P $\leq$ 0.05, ** = P $\leq$ 0.01)

	DCA1	DCA2	DCA3	DCA4
AREA	-0.25	0.56**	-0.25	-0.26
DAYAVE	0.17	0.70**	0.14	-0.05
DAYCV	-0.35*	-0.40*	-0.66**	0.08
DAYPRED	0.17	0.51**	0.62**	0.15
FLDFREQ	-0.25	-0.27	-0.28	-0.15
FLDPRED	0.16	0.04	-0.34*	-0.35*
FLDFREE	-0.06	0.35*	-0.64**	-0.09
BFI	0.09	0.49**	0.65**	0.13
ZERODAY	-0.19	-0.04	-0.50**	-0.08
LOWPRED	0.24	-0.30+	-0.03	-0.03
LOWFREE	0.33+	-0.36*	-0.05	-0.06
Eigenvalue	0.234	0.181	0.130	0.082
Cumulative variance explained	0.37	0.66	0.87	1.00

smallmouth buffalo (SAB) and shortnose gar (SNG) on one end to finescale dace (FND), striped shiner (SRS), blackstripe topminnow (BTM), river redhorse (RRH) and muskellunge (MUE) on the other. Separation along DCA2 is not as dramatic, though SRS and BTM are positioned at one extreme, and RRH and MUE are at the other. The "indicator" species from the 3-level TWINSPAN analysis (see Figure 34) are also indicated in Figure 37. Comparing Figures 37 and 36a reveals that the positions of the species that separate groups 1 and 2 (LSR vs. SDS, BMS, SRL, and QBS) correspond with the positions of the TWINSPAN groups 1 and 2.

Table 17 gives the correlation between the DCA axis scores and the original hydrologic variables. DCA1 was negatively correlated with coefficient of variation and positively correlated with measures of predictable low flows. This suggests that sites with high DCA1 scores (viz., TWINSPAN groups 1 and 2, see Figure 36a) have predictable low flow (LOWFREE) and low variability (DAYCV), whereas sites with low DCA1 scores (groups 3 and 4) are more variable hydrologically. For DCA2, several hydrologic variables showed strong correlations. Low scores on DCA2 correlated with hydrologic variability and unpredictable low flows, and high scores reflected the importance of flow predictability (DAYPRED) and stable baseflow (BFI). This axis essentially separated TWINSPAN groups 1 (low DCA2 = variable) and 2 (high DCA2 = stable) (see Figure 36b). Thus, TWIN 1 and 2 are both relatively stable hydrologically, but TWIN 2 is the more stable of the two. Interestingly, DCA2 also correlated strongly with two static measures of catchment size (Table 17), suggesting that larger streams are more stable. DCA3, which explained about 20% of the overall variation in the site by species analysis, also showed some significant correlations with hydrologic variables. This axis represented a gradient from high variability and low flood predictability to high baseflow stability and overall flow predictability, and it primarily separated TWIN 3 (more variable) from TWIN 4 (higher relative baseflow). In summary, these results indicate that there are major differences among the four TWIN groups in terms of correlations with several hydrologic variables. However, the exact relationship between taxonomic composition and independent hydrologic variables is difficult to sort out, because particular hydrologic variables (DAYCV, DAYPRED, BFI, FLDFREE, and LOWFREE) are significantly correlated with at least two of the first three DCA axes. A multivariate technique that takes into account

multiple correlations among TWINSPAN groups is a superior approach for exploring the taxonomic-hydrologic associations.

The TWINSPAN group identifier for each of the 34 WIMN sites was used in a canonical discriminant analysis (CDA) and discriminant function analysis (DFA). This technique was highly successful in discriminating among the four previously-defined TWIN groups in terms of the independent hydrologic variables. The CDA derived 3 linear combinations of the 9 hydrologic factors that discriminated among the 4 TWINSPAN-defined groups. The first canonical variable was highly significantly different from zero (squared multiple correlation = 0.77, $p < 0.0001$), and both the second and third canonical variables had p-values < 0.10 (Table 18). The individual univariate F-tests for among-group differences on the hydrologic variables showed that BFI, DAYPRED, and DAYCV were highly significant; FLDFREE, FLDPRED and LOWFREE were significant; and, LOWPRED was heavily weighted but not statistically significant (Table 18). The correlations between the canonical variables and the original hydrologic variables (under CAN1, CAN2 and CAN3 in Table 18) showed that the first canonical variable represents a contrast between flow stability (high positive correlation with BFI and DAYPRED) and variability plus predictability of extreme flows (high negative correlation with DAYCV, LOWFREE and FLDFREE). The higher correlations with BFI and DAYPRED indicate that these factors are the most important discriminators among the two groups (also cf. the univariate F-tests). The second canonical variable appears to represent a contrast between sites having high predictability of periods without floods (FLDFREE) and those having low predictability of periods without low flows (LOWFREE). The third canonical variable has high positive correlations with DAYPRED and FLDPRED and high negative correlations with DAYCV, indicating this variable contrasts predictability with variability.

Examination of the mean canonical scores for the 4 TWINSPAN groups of sites shows how the groups differ on each of these synthetic variables. When several canonical variables (and associated original hydrologic variables) are used to discriminate among several classes of sites, it is useful to refer to the univariate F-tests to assist in interpretation of among-group differences. The most important discriminating hydrologic variable is BFI (F = 20.9, CAN1 r = 0.92), and it can be seen that TWIN 1 and 3 have low mean scores on this variable, while TWIN 2 and 4 load heavily on BFI (Table 18). Similarly, TWIN 1 and 3 have high DAYCV, in contrast to TWIN 2 and 4, which have low mean

TABLE 18. SUMMARY OF CANONICAL DISCRIMINANT ANALYSIS (CDA) FOR 4 TWINSPAN-DEFINED GROUPS. GROUP MEANS AND STANDARD DEVIATIONS (IN PARENTHESES) ARE GIVEN FOR EACH HYDROLOGIC VARIABLE, AS ARE RESULTS FOR UNIVARIATE F-TESTS, WHICH INDICATE IF THE FOUR GROUPS DIFFER WITH RESPECT TO HYDROLOGIC VARIABLES. THE CANONICAL VARIABLES REPRESENT WEIGHTED LINEAR RECOMBINATIONS OF HYDROLOGIC VARIABLES THAT MAXIMIZE DISCRIMINATION AMONG ECOLOGICALLY-SIMILAR GROUPS. COEFFICIENTS FOR THE 3 CANONICAL VARIABLES INDICATE CORRELATION BETWEEN THE CANONICAL VARIABLE AND INDIVIDUAL HYDROLOGIC VARIABLES. THE MEAN SCORE FOR EACH ECOLOGICAL GROUP IS ALSO GIVEN FOR THE 3 CANONICAL VARIATES

	TWIN1	TWIN2	TWIN3	TWIN4	$F_{3,30}$	Pr > F	CAN1[*]	CAN2[*]	CAN3[**]
N	7	10	10	7					
DAYCV	169.7	100.0	219.1	124.4	10.4	0.0001	-0.64	0.46	-0.49
	(44.0)	(56.1)	(46.5)	(52.6)					
DAYPRED	47.7	73.0	41.2	69.4	13.2	0.0001	0.76	-0.28	0.48
	(16.8)	(7.3)	(17.7)	(4.0)					
FLDFREQ	0.71	0.66	0.76	0.69	1.1	0.37	-0.25	0.23	-0.24
	(0.21)	(0.07)	(0.15)	(0.09)					
FLDPRED	0.64	0.65	0.66	0.53	3.2	0.039	-0.43	0.07	0.51
	(0.08)	(0.09)	(0.10)	(0.10)					
FLDFREE	0.32	0.37	0.50	0.25	8.4	0.0003	-0.52	0.62	0.36
	(0.11)	(0.13)	(0.07)	0.07					
BFI	0.10	0.37	0.08	0.45	20.9	0.0001	0.92	-0.15	0.22
	(0.07)	(0.16)	(0.11)	(0.09)					
ZERODAY	0.004	0	0.03	0	1.7	0.19	-0.28	0.40	-0.09
	(0.007)	(0)	(0.06)	(0)					
LOWPRED	0.58	0.46	0.48	0.45	2.6	0.074	-0.36	-0.42	-0.16
	(0.11)	(0.07)	(0.11)	(0.09)					
LOWFREE	0.47	0.33	0.34	0.25	6.7	0.001	-0.57	-0.53	0.02
	(0.11)	(0.07)	(0.11)	(0.09)					
Group Mean									
CAN1	-1.77	0.92	-1.49	2.59					
CAN2	-1.56	-0.23	1.26	0.09					
CAN3	-0.41	1.04	-0.12	-0.91					

[*] Squared canonical correlation (= R^2) between CAN1 and hydrologic variables = 0.77 ($F_{27,65}$ = 3.6, p = 0.0001)

[**] Squared canonical correlation (= R^2) between CAN2 and hydrologic variables = 0.53 ($F_{16,46}$ = 2.4, p = 0.01)

[***] Squared canonical correlation (= R^2) between CAN2 and hydrologic variables = 0.37 ($F_{7,24}$ = 2.0, p = 0.09)

scores for DAYCV. Thus, TWIN 1 and 3 are essentially hydrologically "variable" sites, while TWIN 2 and 4 are hydrologically "stable". TWIN 1 sites are separated from TWIN 3 on the second canonical variable (for which these 2 groups have scores of similar magnitude but different sign). TWIN 3 sites are relatively more variable, have longer flood free periods, and shorter lowflow free periods than TWIN 1 sites. The relatively stable TWIN 2 and 4 sites are distinguished in terms of hydrologic variables comprising CAN3 (see Table 18). The univariate F-tests suggest that FLDPRED and overall hydrologic variability (DAYCV and DAYPRED) are primary discriminants for these groups. TWIN 2 sites have significantly higher flood predictability and are less variable generally than the otherwise similar TWIN 4 sites. This indicates that TWIN 2 sites are the most hydrologically stable of the four TWINSPAN groups.

The nonparametric DFA was able to properly classify the 34 sites into the 4 TWINSPAN groups with 100% accuracy. The parametric DFA (which excluded ZERODAY) was only slightly less successful, having a 5% classification error rate.

In addition to the discriminant analysis for the TWINSPAN groups, we used Ward's clustering method to define either 2 or 3 groups of sites from the Jaccard similarity matrix, which essentially expresses the correlation among the 34 sites based on shared species presence (see Methods). In neither the 2-group or the 3-group case was a discriminant function produced from the hydrologic variables that could distinguish among the pre-defined, taxonomically-similar groups. The multivariate test of significance (Wilk's λ) had $p > 0.10$, while the misclassification rate for discriminant function approached 50% (i.e., only 1/2 of the taxonomically-similar groups could be properly discriminated using the hydrologic variables).

Fish Functional Relationships to Hydrologic Factors
When ecological similarity among sites was defined in terms of functional attributes using Ward's method, the CDA and DFA were able to make significant discriminations for both the 2-group and 3-group cases. The hierarchical dendrogram produced by Ward's method is shown in Figure 38. The results of the DFA and CDA are given for the 2-group and 3-group cases in Table 19 and Table 20, respectively. The geographic locations of the 34 WIMN sites coded according to the 3-group case are shown in Figure 30. For the 2-group case,

TABLE 19. SUMMARY OF NONPARAMETRIC CANONICAL DISCRIMINANT ANALYSIS (CDA) FOR 2-CLUSTER CASE. GROUP MEANS AND STANDARD DEVIATIONS (IN PARENTHESES) ARE GIVEN FOR EACH HYDROLOGIC VARIABLE, AS ARE RESULTS FOR UNIVARIATE F-TESTS, WHICH INDICATE IF THE 2 GROUPS DIFFER WITH RESPECT TO HYDROLOGIC VARIABLES. THE CANONICAL VARIABLE REPRESENTS A WEIGHTED LINEAR RECOMBINATION OF HYDROLOGIC VARIABLES THAT MAXIMIZE DISCRIMINATION AMONG ECOLOGICALLY-SIMILAR GROUPS. COEFFICIENTS FOR CAN1 INDICATE CORRELATION BETWEEN THE CANONICAL VARIABLE AND INDIVIDUAL HYDROLOGIC VARIABLES. THE MEAN SCORE FOR EACH ECOLOGICAL GROUP IS ALSO GIVEN FOR THE CANONICAL VARIABLE

	Group 1 (Variable)	Group 2 (Stable)	$F_{1,32}$	Pr > F	CAN1*
N	16	18			
DAYCV	173.5 (73.7)	137.2 (60.7)	2.48	0.13	-0.333
DAYPRED	46.5 (19.9)	67.7 (11.1)	15.08	0.0005	0.704
FLDFREQ	0.75 (0.17)	0.67 (0.09)	2.68	0.11	-0.346
FLDPRED	0.63 (0.10)	0.62 (0.10)	0.15	0.70	-0.087
FLDFREE	0.37 (0.13)	0.37 (0.14)	0.01	0.91	0.026
BFI	0.16 (0.19)	0.32 (0.17)	6.78	0.014	0.520
ZERODAY	0.02 (0.05)	0.0001 (0.0003)	2.91	0.10	-0.360
LOWPRED	0.49 (0.14)	0.49 (0.08)	0.01	0.94	-0.018
LOWFREE	0.35 (0.14)	0.34 (0.10)	0.03	0.87	-0.037
Group Mean CAN1	-1.391	1.237			

* Squared canonical correlation (= R^2) between CAN1 and hydrologic variables = 0.646 ($F_{9,24}$ = 4.87, p = 0.0009)

the 34 sites were separated into groups of 16 and 18 (cf. all circles to triangles in Figure 30; see also Figure 38). The CDA derived a linear combination of the 9 hydrologic factors that discriminated among the groups, and this canonical variable was highly significantly different from zero (squared multiple correlation different from zero (squared multiple correlation = 0.648, p = 0.0009). The individual univariate F-tests for among-group differences on the hydrologic variables showed that DAYPRED and BFI were highly significant, while ZERODAY, DAYCV and FLDFREQ were heavily

TABLE 20. SUMMARY OF CANONICAL DISCRIMINANT ANALYSIS (CDA) FOR 3-CLUSTER CASE. GROUP MEANS AND STANDARD DEVIATIONS (IN PARENTHESES) ARE GIVEN FOR EACH HYDROLOGIC VARIABLE, AS ARE RESULTS FOR UNIVARIATE F-TESTS, WHICH INDICATE IF THE THREE GROUPS DIFFER WITH RESPECT TO HYDROLOGIC VARIBLES. THE CANONICAL VARIABLES REPRESENT WEIGHTED LINEAR RECOMBINATIONS OF HYDROLOGIC VARIABLES THAT MAXIMIZE DISCRIMINATION AMONG ECOLOGICALLY-SIMILAR GROUPS. COEFFICIENTS FOR CAN1 AND CAN2 INDICATE CORRELATION BETWEEN THE CANONICAL VARIABLE AND INDIVIDUAL HYDROLOGIC VARIABLES. THE MEAN SCORE FOR EACH ECOLOGICAL GROUP IS ALSO GIVEN FOR THE TWO CANONICAL VARIATES

	Group 1 (Unstable)	Group 2 (Moderately Stable)	Group 3 (Very Stable)	$F_{2,31}$	Pr > F	CAN1*	CAN2*
N	16	10	8				
DAYCV	173.4 (73.7)	161.0 (52.9)	107.5 (59.5)	2.82	0.075	-0.334	0.506
DAYPRED	46.5 (19.9)	63.8 (12.0)	72.5 (8.2)	8.28	0.001	0.704	-0.295
FLDFREQ	0.75 (0.17)	0.67 (0.10)	0.67 (0.07)	1.30	0.29	-0.346	-0.015
FLDPRED	0.63 (0.10)	0.62 (0.12)	0.62 (0.07)	0.08	0.92	-0.086	-0.031
FLDFREE	0.37 (0.13)	0.35 (0.18)	0.40 (0.09)	0.25	0.78	0.026	-0.219
BFI	0.16 (0.19)	0.30 (0.18)	0.35 (0.17)	3.52	0.042	0.520	-0.179
ZERODAY	0.02 (0.05)	0.0001 (0.0004)	0.0 (0.0)	1.41	0.26	-0.359	-0.002
LOWPRED	0.49 (0.14)	0.50 (0.08)	0.48 (0.09)	0.08	0.92	-0.018	0.125
LOWFREE	0.35 (0.14)	0.35 (0.12)	0.33 (0.07)	0.05	0.96	-0.037	0.073
Group Mean CAN1	-1.37	1.22	1.22				
CAN2	-0.001	0.80	-1.00				

* Squared canonical correlation (= R^2) between CAN1 and hydrologic variables = 0.646 ($F_{18,46}$ = 2.65, p = 0.004)

** Squared canonical correlation (= R^2) between CAN2 and hydrologic variables = 0.319 ($F_{8,24}$ = 1.40, p = 0.246)

ted but not statistically significant (Table 19). The correlations between the canonical variable and the original hydrologic variables (under CAN1 in Table 19) show that the canonical variable represents a contrast between flow stability (high positive correlation with DAYPRED and BFI) and extreme flows and variability (high negative correlation with DAYCV, ZERODAY and FLDFREQ). The higher correlations with DAYPRED and BFI indicate that these factors are the most important discriminators among the two groups (also cf. the univariate F-tests). The mean scores for the two groups of sites on the canonical variable (CAN1) are of similar magnitude but opposite sign. The negative coefficient for group 1 (-1.39) indicates that these 16 sites are inversely correlated with DAYPRED and BFI and positively correlated with DAYCV, ZERODAY and FLDFREQ. Group 1 sites can thus be characterized as hydrologically "variable" sites. By contrast, the group two mean score (+1.24) on CAN1 indicates that these 18 sites can be characterized as hydrologically "stable". The nonparametric DFA was able to properly classify the 34 sites into the two groups with 100% accuracy. The parametric DFA (which excluded ZERODAY) was less successful, having a 12% classification error rate. However, the parametric DFA also identified DAYPRED and BFI as the two most important environmental factors in discriminating among the two ecological groups. As in the non-parametric analysis, DAYCV and FLDFREQ were less heavily weighted but substantially negatively correlated with CAN1. The squared multiple correlation between CAN1 and the hydrological variables was 0.633 (p = 0.0005).

The location of individual sites (coded by ecological group) as a function of individual scores on the canonical variable is shown in Figure 39. There is some overlap in this 1-dimensional representation of a 9-dimensional hydrologic space. The sites can also be viewed in the bivariate space of the two major hydrologic factors (DAYPRED and BFI) that contribute to CAN1 (Figure 40). The group centroids are clearly separated, although there is some overlap in these two dimensions among the individual sites. Additions of additional axes (i.e., variables with high weight on CAN1) would further separate the clusters from one another.

For the 3-group case, sites were separated into clusters of 16, 10 and 8, with the last two groups representing a splitting of the 18 member "stable" group from the 2-cluster case (see Figures 30, 38). The CDA derived linear combinations of the 9 hydrologic factors that discriminated among the three

groups (Table 20). The first canonical variable was highly significantly different from zero (squared multiple correlation = 0.646, p = 0.004), while the second was not (correlation = 0.319, p = 0.246). This result indicates that CAN2 explained little additional separation among the groups not described by CAN1, probably because the same hydrologic variables were most heavily weighted on both canonical variables. Nonetheless, the individual sites in the three groups can be reasonably well distinguished when plotted in the space generated by CAN1 and CAN2 (Figure 41). The individual univariate F-tests for among-group differences on the hydrologic variables showed that DAYPRED and BFI were significant (p < 0.05) and DAYCV approached significance (p = 0.075) (Table 20). The correlations between the canonical variables and the original hydrologic variables on CAN1 were identical (by definition) to those in the 2-group case. For the second canonical variable (CAN2), there was a high positive correlation with DAYCV and a relatively large negative correlation with DAYPRED. CAN1 thus represents a contrast between flow stability (high positive DAYPRED and BFI) and variability and flow extremes (negative DAYCV, ZERODAY and FLDFREQ). CAN2 represents a contrast between flow variability (high positive DAYCV) and flow predictability (negative DAYPRED) (see Figure 41). Group 1 sites are identical to those in the 2-case solution, having a high negative mean score on CAN1 (see Table 20). They are characterized as hydrologically "variable". Group 2 and Group 3 sites both have a high positive mean score on CAN1, indicative of hydrologic stability, but they are discriminated on CAN2. Group 2 sites score positively on CAN2 (indicating high relative variability), but group 3 sites score negatively on CAN2 (indicating low variability). Thus, the 10 sites in group 2 can be characterized as hydrologically "moderately stable", whereas the 8 sites in group 3 are hydrologically "very stable".

The nonparametric discriminant function analysis (DFA) was able to use the hydrologic data to properly classify the 34 sites into their respective ecological groups with 100% accuracy. The parametric DFA (which excluded ZERODAY) was only slightly less successful, having a 2% classification error rate. The parametric DFA also identified DAYPRED, BFI, and DAYCV as the most important hydrological factors in discriminating among the 3 ecological groups. The squared multiple correlation for CAN1 was 0.635 (p = 0.0037), but the value for CAN2 (0.248) was not significant (p = 0.35).

Possible Confounding Factors Influencing Results

The potential confounding of the hydrological-ecological patterns by sampling intensity (Figure 31) and catchment area (Figure 33) was assessed by examining whether the defined groups of sites differed with respect to these factors. Figure 42 shows that both groups of ecologically-similar sites express a strong but very similar relationship between number of species collected and sampling intensity at each site. We can conclude that the observed differences among groups with respect to functional organization is not an artifact of differential sampling intensity among the two types of streams. Systematic relationships between cluster affiliation and the measures of stream size can be viewed in several ways. Figure 43a shows that there are no consistent differences between groups in terms of the species collected and upstream catchment area. However, when area is defined in terms of average discharge (Figure 43b), the variable streams show a species-area relation, while the stable group does not, due mostly to larger streams having fewer species collected. But when stream size is defined as suggested by Hughes and Omernik (1983) as mean annual runoff (mm/yr), both groups of sites show similar species-area relations (Figure 43c). These alternative descriptions support the conclusion that the ecologically-defined groups are not "predictable" in terms of knowledge of catchment area alone. For the 3-group case, neither the moderately stable nor the very stable sites showed a strong relationship between species richness and either catchment area (Figure 44a) or average discharge (Figure 44b). However, there was a tendency for sampling intensity of streams to vary as a function of size (Figure 45). With the exception of one point, small streams typically were sampled more frequently than large streams, leading to a higher apparent richness in the small streams than might otherwise be expected.

Functional Organization of Ecologically-similar Assemblages

Several interesting and consistent patterns emerged when the functional composition of fish assemblages were contrasted with corresponding hydrologic characteristics for the 34 WIMN sites. These differences are summarized in a general fashion in Figure 46. To investigate the relative contributions of the various functional attributes to defining the ecologically-similar groups, we compared means and standard errors of the individual functional attributes for each group using oneway analysis of variance. The parametric and non-

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parametric anovas produced very similar results; therefore, only the parametric results are reported here. This univariate approach shows major differences among groups and provides the basis for the generalizations illustrated in Figure 46. However, many of the functional variables were highly cross-correlated (Table 21), a fact that supports the use of the multivariate canonical discriminant analysis described previously. The taxonomic composition of the assemblages from the 3 hydrological stream types also varied (Table 22, Figure 46). Differences in taxonomic composition help explain the observed functional patterns, since the functional attributes were generated from species-specific information initially.

Morphological Variables--

When two groups of functionally-similar assemblages were created, several interesting observations were made. First, no substantial among-group differences were apparent for the first morphological variable (swimming factor), but fishes from variable habitats had significantly lower values (p = 0.03) on the second morphological variable, the shape factor (Figure 47a). High scores on the shape factor reflect a relatively elongated body shape that presumably enhances hydrodynamic profile and reduces energetic costs of position-maintenance in fast-flowing water (Webb and Weihs 1986).

For the 3-group case, again no differences on the swimming factor were found, while some separation on the shape factor was observed (Figure 47b). Highly significant differences (p < 0.0001) in the shape factor were observed among groups, with assemblages from the very stable streams showing greatest body elongation compared to assemblages from the stable and variable streams, which did not differ from one another (Figure 47b).

Trophic Variables--

For the 2-cluster case, several among-group differences were observed for trophic categories (Figure 48a). Assemblages in hydrologically variable streams had a significantly greater abundance of omnivores (p = 0.0005) and a significantly lower abundance of benthic invertivores (p = 0.0001) than the stable streams. Generalist invertivores were also more abundant (p = 0.07) in variable streams, while parasitic species were less abundant (p = 0.06). Planktivores, which were recorded only from the variable sites, were significantly more abundant there than in the stable sites (p = 0.014). (This

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TABLE 21. PEARSON CORRELATION MATRIX FOR 25 FUNCTIONAL ATTRIBUTE VARIABLES FOR 106 SPECIES GROUPED ACCORDING TO 5 MAJOR CATEGORIES (SEE TABLE 11). R-VALUES WITH P < 0.05 USING A BONFERRONI TEST AND ARE INDICATED BY BOLDFACE AND "*". FOR P < 0.10, "a" IS USED

	SWIM	SHAPE	HERB	OMNIVOR	GENERAL	SURFACE	BENTHIC	PISCIV	PLANK	PARASIT
MORPHOLOGY										
SWIM	1.000									
TROPHIC										
HERB	0.109	0.045	1.000							
OMNIVOR	-0.229	-0.357	-0.357	1.000						
GENERAL	0.014	-0.569	0.000	0.466	1.000					
SURFACE	0.733*	-0.062	0.006	-0.412	-0.194	1.000				
BENTHIC	-0.079	0.454	0.187	-0.612*	-0.593[a]	0.048	1.000			
PISCIV	-0.095	0.316	-0.334	-0.410	-0.523	0.072	-0.029	1.000		
PLANK	0.123	-0.176	-0.071	0.006	-0.040	-0.080	-0.258	0.243	1.000	
WATER 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[a]	0.304	-0.423	-0.568	0.014	0.587[a]	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
STREAM SIZE										
SMALL	-0.380	-0.048	-0.361	0.815*	0.304	-0.376	-0.321	-0.399	-0.292	-0.224
LARGE	0.235	0.168	0.130	-0.691*	-0.369	0.317	0.659	0.135	-0.077	0.257
GENERAL	0.196	-0.210	0.332	-0.082	0.204	0.079	-0.455	0.184	0.384	-0.171
TOLERANCE										
TOLERANT	0.002	-0.604*	-0.272	0.832*	0.592[a]	-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
INTOL	-0.286	0.354	-0.081	-0.506	-0.450	-0.150	0.714*	0.302	-0.191	0.362

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TABLE 21 (continued)

	FAST	MODERATE	SLOW	GENERAL	RUBBLE	SAND	SILT	GENERAL
WATER VELOCITY								
FAST	1.000							
MODERATE	0.357	1.000						
SLOW	-0.726*	-0.846*	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	
STREAM SIZE								
SMALL	-0.093	-0.254	0.167	0.104	-0.204	0.071	0.448	-0.190
LARGE	0.298	0.479	-0.432	0.027	0.441	-0.299	-0.607	0.149
GENERAL	-0.177	-0.317	0.316	-0.151	-0.276	0.384	0.199	-0.011
TOLERANCE								
TOLERANT	-0.437	-0.560	0.585[a]	-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
INTOL	0.499	0.451	-0.627	0.447	0.660	-0.525	-0.670*	-0.036

	SMALL	LARGE	GENERAL	LAKE	TOLERANT	MODERATE	INTOL
STREAM SIZE							
SMALL	1.000						
LARGE	-0.664*	1.000					
GENERAL	-0.349	-0.448	1.000				
TOLERANCE							
TOLERANT	0.590[a]	-0.605*	0.095	0.025	1.000		
MODERATE	-0.134	-0.171	0.412	-0.101	0.129	1.000	
INTOL	-0.307	0.564	-0.385	0.006	-0.675*	-0.765*	1.000

TABLE 22. RELATIVE PROPORTIONS OF 41 DOMINANT FISH SPECIES FOR 34 WIMN SITES FOR E OF THREE HYDROLOGICAL STREAM TYPES. SPECIES ARE RANKED ACCORDING TO THE TOTAL NUMBER OF SITES AT WHICH EACH SPECIES OCCURS. ONLY SPECIES HAVING A RELATIVE PROPORTION $\geq$0.500 IN AT LEAST ONE STREAM TYPE ARE INCLUDED. SPECIES SHOWN IN FIGURE 37 ARE INDICATED BY A "*"

Abbrev.	Common Name	Total Sites	Variable	Moderately Stable	Very Stable	
BDD	BANDED DARTER	13	.250	.600	.375	
BKB	BLACK BULLHEAD	18	.750	.400	.250	*
BLC	BLACK CRAPPIE	12	.375	.200	.500	
BLG	BLUEGILL	17	.562	.500	.375	
BLM	BLUNTNOSE MINNOW	30	.938	.900	.750	
BNT	BROWN TROUT	13	.375	.400	.375	
BMS	BIGMOUTH SHINER	20	.562	.700	.500	
BND	BLACKNOSE DACE	18	.625	.400	.500	
BSD	BLACKSIDE DARTER	23	.625	.500	1.000	
CAP	CARP	24	.812	.700	.500	
CCF	CHANNEL CATFISH	10	.250	.500	.125	
CHL	CHESTNUT LAMPREY	5	.062	.000	.500	
CRC	CREEK CHUB	33	1.000	1.000	.875	
CSH	COMMON SHINER	34	1.000	1.000	1.000	
EMS	EMERALD SHINER	14	.500	.500	.125	
FHM	FATHEAD MINNOW	24	.938	.700	.250	
FTD	FANTAIL DARTER	17	.438	.600	.500	
GLR	GOLDEN REDHORSE	19	.438	.600	.750	
GOS	GOLDEN SHINER	8	.500	.000	.000	*
GSF	GREEN SUNFISH	18	.625	.700	.125	
HHC	HORNYHEAD CHUB	26	.688	.700	1.000	
JND	JOHNNY DARTER	30	.938	.900	.750	
LGP	LOGPERCH	10	.188	.100	.750	
LND	LONGNOSE DACE	16	.250	.600	.750	*
LSR	LARGESCALE STONEROLLER	10	.125	.100	.875	
NHS	NORTHERN HOGSUCKER	16	.188	.500	1.000	*
NOP	NORTHERN PIKE	24	.812	.500	.750	
PMK	PUMPKINSEED	11	.500	.100	.250	*
RKB	ROCK BASS	15	.375	.500	.500	
ROS	ROSYFACE SHINER	14	.188	.700	.500	*
SKM	SUCKERMOUTH MINNOW	8	.125	.600	.000	
SLR	SILVER REDHORSE	18	.438	.500	.750	
SPS	SPOTFIN SHINER	23	.688	.900	.375	
SCT	STONECAT	22	.562	.900	.500	
SHR	SHORTHEAD REDHORSE	21	.312	.800	1.000	*
SDS	SAND SHINER	21	.688	.800	.250	
SMB	SMALLMOUTH BASS	20	.312	.800	.875	*
WAE	WALLEYE	18	.438	.500	.750	
WTS	WHITE SUCKER	33	.938	1.000	1.000	
YEB	YELLOW BULLHEAD	9	.500	.100	.000	*
YEP	YELLOW PERCH	14	.625	.100	.375	*

result held when a non-parametric test was employed.) These are consistent patterns that suggest that generalist trophic strategies are associated with hydrologic variability in the study streams.

In the 3-cluster case, further separation of the stable and the very stable sites occurred on these trophic attributes (Figure 48b). The very stable sites had more benthic invertivores ($p < 0.0001$), fewer generalist invertivores ($p = 0.0002$) and more parasitic fish ($p = 0.0004$) than the stable or variable sites. Very stable sites also had the fewest omnivores, though this difference was not significantly different from omnivore proportion at moderately stable sites.

Substrate Preference--

For the 2-group case, assemblages in variable streams had relatively few species associated with rubble ($p < 0.0001$) and more species typically associated with silt ($p < 0.0001$). There was a tendency for substrate generalists to be more highly represented in variable streams, but this difference was not significant ($p = 0.09$) (Figure 49a).

When the stable streams were further divided in the 3-group case (Figure 49b), we observed that significant differences in species associated with rubble and silt still occurred among the three stream types ($p < 0.0001$ for both), but the very stable sites were not significantly different from the moderately stable sites ($p > 0.05$). However, the proportion of sand-associated species at very stable sites was significantly lower ($p = 0.004$) than at the moderately stable or variable sites, which did not differ from one another (Figure 49b).

Stream Size Association--

For this macro-habitat attribute, the major contrast between the groups in the 2-cluster case was that variable sites had significantly more small stream fishes ($p = 0.05$) and lake fishes ($p = 0.05$), while stable streams had more fishes found in medium-large systems ($p = 0.0006$) (Figure 50a). Variable streams also tended to have more generalist, small-large system fishes, though this difference was not statistically significant ($p = 0.16$).

For the 3-cluster case, the very stable streams showed a significantly greater proportion of fishes typical of medium-large systems ($p = 0.0002$) and a lower proportion of generalist fishes typical of small-large systems ($p =$

0.004) (Figure 50b). Lake species were absent from moderately stable streams, which had significantly fewer (p = 0.017) of these species than very stable or variable streams.

Biotope (Water Movement) Association--

The dominant pattern observed for the 2-cluster case for this functional variable was the high representation of slow water species (p = 0.0001) at variable sites (Figure 51a). Stable sites had more fish species associated with fast (p = 0.0001) and intermediate (p = 0.004) velocity macrohabitats. There was a tendency (p = 0.08) for stable habitats to have more generalist species.

For the 3-cluster case, stream assemblages from very stable streams had proportionally more medium-velocity species (p = 0.0004) than did either moderately stable or variable streams (Figure 51b). Very stable streams also had significantly fewer slow-velocity fishes than moderately stable streams, which themselves were significantly different from the variable streams. No significant differences among moderately stable and very stable streams were observed for the fast or general categories (Figure 51b).

Environmental Tolerance--

Fish assemblages in variable systems had much higher proportions of tolerant (p < 0.0001) and moderately tolerant (p = 0.02) species relative to stable systems, which had a high proportion of intolerant species (p < 0.0001) (Figure 52a).

In the 3-cluster case, fish assemblages from the three groups fell along a tolerant-intolerant gradient, with very stable sites having significantly fewer tolerant species (p < 0.0001) and more intolerant species (p = 0.0001) than variable sites. Moderately stable sites were intermediate and significantly distinct from the variable and the very stable sites (Figure 52b).

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DISCUSSION

The results of this analysis clearly show that differences in fish
assemblage structure are strongly associated with specific hydrologic factors
that vary among catchments across geographic scales. We interpret this
pattern to mean that hydrologic regime constrains assemblage structure,
defined in either functional or taxonomic terms. Thus, given knowledge of
critical hydrologic factors for a stream in the geographic area covered by
this study, certain general features of the fish community should be
predictable with some confidence.

Several previous studies have related fish community structure to
habitat variables (e.g., Gorman and Karr 1978, Schlosser 1985, 1987,
Angermeier 1987, Hawkes et al. 1986, Bisson et al. 1988, Rahel and Hubert
1991, Bozek and Hubert 1992, Nelson et al. 1992, Pearsons et al. 1992), and
the influence of hydrologic variation (particularly floods) on fish community
structure has been amply documented (e.g., John 1963, Harrell 1978, Meffe
1984, Matthews 1986, Coon 1987, Schlosser 1987, Bain et al. 1988, Jowett and
Duncan 1990, Fausch and Bramblett 1991). This study represents one of the
only attempts to identify cross-stream patterns in fish assemblage structure
based solely in terms of long-term hydrologic averages (also see Horwitz
1978), and it is the only research of which we are aware that uses multiple
measures of hydrologic variability. Further, while others have developed
functional descriptions for fish species to assess assemblage response to
catchment degradation (Karr et al. 1986), this is the first study we are aware
of that describes fish assemblage structure in functional terms designed to be
sensitive to hydrologic variation.

A hierarchical classification (using TWINSPAN) of the fish assemblage
data defined in taxonomic terms identified two major divisions of sites (TWIN
1 + 2 and TWIN 3 + 4). These two divisions could be further separated into
four groups with relatively distinct geographic separation (Figure 35).
Canonical discriminant analysis (CDA) showed that these four groups had
significant hydrologic correlates, but the interesting result was that neither
the two most hydrologically "stable" groups (TWIN 2 and 4) nor the two most
hydrologically "variable" groups (TWIN 1 and 3) occurred in the same major
division (cf. Table 18 and Figure 34). This result suggests the possibility
that, within a taxonomically-similar major division (e.g., TWIN 1 + 2 or TWIN

3 + 4), taxa are further segregated among available sites depending on catchment-scale hydrologic conditions. This possibility assumes that there is no confounding of potential range limits of fish species and the geographic distribution of sites having specified hydrologic characteristics. In other words, if taxonomically-similar fish assemblages in a major division (e.g., TWIN 1 + 2 sites) have ranges that potentially include all 17 of the sites in that division, then the null expectation would be a random distribution of these species among all 17 of the sites. To assess the range of fish species distributions in the region covered by this study, one of us (NLP) identified 19 species that were present in >50% of the sites in at least one of the four TWINSPAN groups. The selected species included all the "indicator" species shown in Figure 34. Without prior knowledge of the TWINSPAN or hydrologic affiliation, the other of us (JDA) examined geographic range maps for these species (using Lee et al. 1980) and attempted to assign fish species to the four TWINSPAN groups. For only 7/19 species could geographic ranges be reasonably related to the four TWINSPAN groups (BMS, GOS, SRL, LKC, QBS, LSR, and YEP). The best that could be said for each of these seven species was that it was unlikely to occur in one particular TWINSPAN group. Of these seven, only three (BMS, QBS, and LSR) were correctly identified as being absent from one particular TWINSPAN group. The fact that these three species are "indicator" species separating TWIN 1 + 2 from TWIN 3 + 4 (Figure 34) suggests some zoogeographic constraint among the first two major TWINSPAN divisions. However, within each major division (i.e., four TWINSPAN groups), it appears that all species can potentially occupy all 17 sites. That they do not suggests that the recorded distribution reflects some process of site selection (or site exclusion) that is correlated with site hydrologic factors.

When viewed in functional terms, the relationship between fish assemblage structure and hydrologic regime across the 34 WIMN sites is remarkably clear (Figure 30), and assemblages can be described as coming from hydrologically "variable", "moderately stable", and "very stable" sites. The geographic distribution of the functionally-defined assemblages complements the geographic distribution of the taxonomically-defined assemblages, thus providing further evidence for hydrologic constraints on assemblage structure. This can be seen by comparing, on the one hand, the distribution of the 16 hydrologically "variable" sites in the functional analysis (triangles in Figure 30) to the 17 "variable" sites in the taxonomic analysis (TWIN 1 + 3 in

TABLE 23. CROSS-CLASSIFICAION OF HYDROLOGIC DESIGNATIONS
FOR THE 34 WIMN SITES DEFINED IN TAXONOMIC VS.
FUNCTIONAL TERMS

Taxonomic Designation	Functional Designation		
	Variable (n=16)	Moderately Stable (n=10)	Very Stable (n=8)
"Variable" sites			
TWIN 1 (n=7)	6	1	0
TWIN 3 (n=10)	6	4	0
"Stable" sites			
TWIN 2 (n=10)	1	1	8
TWIN 4 (n=7)	3	4	0

Figure 35), and, on the other hand, the distribution of the 18 "stable" functional sites (combined moderately stable and very stable sites in Figure 30) to the 17 "stable" taxonomic sites (TWIN 2 + 4 in Figure 35). The results of this comparison are summarized in Table 23, which shows that, while the hydrologic designation for sites defined in functional terms do not precisely correspond with the hydrologic designation for the taxonomically-defined sites, the 2-group functional analysis largely identifies the four taxonomically-defined assemblages coming from "variable" and "stable" streams. For the variable functional sites, 75% (12/16) of the taxonomic sites were similarly classified, and for the stable (moderately stable + very stable) functional sites, 72% (13/18) were similarly classified. TWIN 1 and TWIN 2 groups were the most similar in hydrologic designation to the corresponding functionally-defined sites (Table 23). This functional approach thus suggests a powerful technique that can be used to generalize across zoogeographic boundaries.

The advantage of characterizing fish assemblages in terms of functional composition is that this approach provides ecological insight that are difficult to acquire by taxonomic approaches alone. The functional approach,

combined with species presence/absence data, allows *coarse-grain patterns* to be detected when the corresponding hydrologic data is also coarse-grained (e.g., long-term averages of hydrologic variables). More detailed hydrological information would probably be needed to detect fine-grained ecological patterns such as inter-annual variation in population abundances or size structure.

The contrasts in functional characteristics for fish assemblages in hydrologically variable vs. stable streams (Figures 17-22) were largely in keeping with theoretical expectations. In many instances, fish assemblages showed differences for functional attributes that varied consistently with average hydrologic environment. This held for both the 2-cluster case (variable vs. stable contrast) and the 3-cluster case (variable to moderately stable to very stable gradient). The most striking pattern was that assemblages from hydrologically variable streams had generalized feeding strategies, were associated with silt and general substrates, were characterized by slow-velocity species with headwater affinities, and were broadly tolerant. By contrast, stable and very stable streams had less tolerant assemblages, more specialized trophic guilds and species associated with fast-flowing and/or permanent streams (see Figure 46). Many of the differences among the stream groups for individual functional attributes might be expected given the correlation structure of the functional data (see Table 21). However, the ecological significance of these results is that the patterns, taken as a whole, are consistent with the general theoretical expectation that variable systems are dominated more by generalists (trophic, habitat) and tolerant species than stable systems. These broad differences in functional organization reflect differences in species composition across the sites (see Figure 46, Table 22). Variable streams are dominated by generally tolerant species of ictalurids (brown and yellow bullhead), percids (yellow perch), cyprinids (golden shiner), and centrarchids (pumpkinseed). By contrast, stable sites are characterized by more elongate, less tolerant catostomids (northern hogsucker, shorthead redhorse), cyprinids (rosyface shiner, longnose dace) and a centrarchid (smallmouth bass).

The finding that assemblages from hydrologically variable streams contain more small-stream and wide-ranging species (Figure 50) offers an intriguing possible interpretation. To the extent that flow variability and low baseflow (see scores on the first canonical variables in Tables V and VI)

typify the variable streams, one might expect these sites to be comprised of the "colonizing" headwater species that Schlosser (1987) identified as adapted to variable headwater environments in temperate warmwater streams of the central United States. Interestingly, these functional "headwater" sites are not comprised only of the smaller streams in the WIMN dataset (e.g., compare multiple measures of area in variable vs. stable sites in Figure 43), suggesting that stream size may not be the sole correlate of species' adaptive strategies employed by species in hydrologically-variable sites. Additional life history information would be desirable to explore this pattern.

Some interesting possible environmental correlates of variable vs. stable streams can be inferred. In an extensive survey of New Zealand streams, Jowett and Duncan (1990) found that several physical characteristics were related to flow variability. Compared to stable streams, systems with high flow variability had much lower velocities (under average discharge conditions), which probably resulted in higher average water temperatures. Variable-flow streams were more complex morphologically, having well-developed pool-riffle structures where pools were deeper and riffles shallower than the stable stream systems. If these patterns hold for the WIMN streams, then the high relative proportion of generalist and tolerant species in the variable streams would be explicable. Coon (1987) studied fish communities at two locations on the South Branch Root River in Minnesota, and found that an upstream site was flashier than the downstream site, owing to greater relative impermeability of the basin in the upstream reaches. 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 WIMN sites considered in this paper. Specifically, the very stable hydrologic sites in this study (Table 16) may be characterized by high groundwater inflow and relatively sparse ice cover in winter and minimal oxygen stress in summer. By contrast, the variable hydrologic sites may represent relatively harsh sites in terms of winter ice, low summer water velocities, and associated seasonal thermal/oxygen stress.

The absence of a strong species-area relationship suggests a potential limitation of this study. Species-area relationships have been documented in many systems, but the strength of the relationship may depend on the units

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used to define area. For example, Angermeier and Schlosser (1989) found habitat volume to be a better predictor of number of species than habitat area, while Watters (1992) found a tight species-area relationship for fishes in 37 Ohio River drainages based on catchment area alone. A contributing factor to the absence of a species-area relation in the present study appears to be the differential sampling intensity of streams varying in size (Figure 45). Generally, small streams were sampled more frequently than large streams, leading to a tendency toward higher apparent richness in the small streams (cf. Figure 44). Given the strong relationship between sampling intensity, species collected, and catchment area in this study, we suspect that a species-area relation would exist for the WIMN sites had all sites been sampled with equal effort. However, the fact that the ecologically-similar groups of assemblages identified in this study showed *similar* species-area and species-sampling intensity relationships provides support for the argument that the hydrological-ecological patterns documented here are not simply an artifact of the sampling limitations. A further point worth emphasizing is that species-area relationships may themselves reflect hydrologic variability. For example, Angermeier and Schlosser (1989) documented that species-area relationships were stronger in Panamanian than in northern temperate zone streams (in Minnesota and Illinois). They noted that the temperate streams were characterized by frequent shifts between physically harsh and benign environmental conditions, and they suggested that the community organization in these streams was predominantly influenced by immigration/extinction dynamics, which tend to mask species-area relations as mobile opportunists continually move into and out of available habitats. These dynamic processes could contribute, in part, to the absence of clear species-area relations in the WIMN streams. However, if environmental variability masks the species-area relationship, then we would expect to see a stronger species-area relationship expressed in the stable streams, yet this was not observed (see Figure 44). The question of the relationship between species-area curves and hydrologic variability deserves closer attention in future research.

One of the most interesting findings of this analysis is that functional species traits provide theoretically interpretable insight into assemblage structure in differentially-variable environments that goes beyond strictly taxonomic information. This result provides some corroboration for Southwood's (1977) "habitat templet" hypothesis, which has been recently

proposed as particularly relevant for lotic ecosystems (Minshall 1988, Poff and Ward 1989, 1990, Schlosser 1990, Poff 1992a, Townsend and Hildrew 1993). Thus, a speculative application of our results would suggest that an alteration in hydrologic regime may lead to adjustments in assemblage structure. The use of functional species traits may be a more powerful tool for projecting the potential assemblage repsonse to such broad scale change than would traditional taxonomic approaches, because generalization across zoogegraphic domains is possible.

These results are of particular interest in the context of climatic change, which, at regional scales, is expected to alter precipitation-runoff regimes, thereby modifying stream hydrology and community structure (see Grimm 1992, Poff 1992b). For example, Tonn (1990) argued that changes in local fish fauna in response to climate change are less likely if assemblages are drawn primarily from a regional species pool comprised of generalists, which are more broadly tolerant across a range of environmental parameters. Generalist fish species typically do better than specialists in invading new habitats (Holdgate 1986), and specialist fish species that invade temporally variable habitats may neither persist (Meffe 1984) nor modify community structure of the invaded habitat (Zaret 1982). These considerations suggest that climate change which increases environmental harshness or variability should favor generalist species. Several scenarios can be put forth that would increase environmental variability and/or harshness in WIMN streams (see Section 1 of this report). Decreased precipitation, coupled with higher regional temperatures, would reduce habitat volume and presumably increase physiological stress for stream fishes. Increases in frequency or duration of hydrologic extremes is one predicted consequence of climate change (Rind 1989), and such changes would presumably favor generalist species. However, for any particular region, great uncertainty exists in terms of predicting how hydrologic regimes are likely to change. For example, precipitation in climatically-distinct regions may change by $\pm$ 20% and runoff may change by $\pm$ 50% (Schneider et al. 1990). Thus, were the Wisconsin-Minnesota area to become wetter over the coming decades, generalist species might not gain any advantage.

The results of this study on 34 WIMN streams are encouraging for laying the groundwork for more detailed and definitive studies that explore the relationship between stream fish community structure and hydrologic

variability. Given some of the problems associated with the dataset used in this study, we caution against *concluding* that this study demonstrably shows that a specified change in climate will have a specified ecological consequence. Additional studies of this sort are needed before such a conclusion is justified, even for the upper Midwest region. Future work should focus on satisfying several criteria: collect fish data with equivalent sampling intensity and techniques; record numerical abundances of species (not just presence/absence); estimate population size structure; collect samples over the same time periods (years); record local habitat characteristics (e.g., depth, width, velocity, temperature) where samples are collected; and ensure that hydrologic data of similar duration are available. When applied to multiple sites across a broad geographic scale, studies that satisfy these criteria have the potential to reveal important community-environment patterns that can assist resource scientists in mitigating the adverse impacts associated with rapid climate change.

CONCLUSIONS AND RECOMMENDATIONS

Stream fish assemblage data (presence/absence) were collected from 34 sites in Wisconsin and Minnesota where long-term hydrologic data also existed. Fish assemblages were analyzed both in terms of taxonomic and functional organization, and ecologically-similar groups were identified for both and then related to independent hydrologic factors using multivariate statistical techniques. The taxonomic analysis (using TWINSPAN) showed strong geographic patterns among taxonomically-similar groups. Zoogeographic patterns (inferred from species range maps) played some role in dividing the 34 assemblages into two major groups, but further division into four taxonomically-defined groups of assemblages reflected hydrologic factors, not zoogeographic constraints. The functional analysis of the 34 fish assemblages revealed that two or three groups of sites could be defined in terms of functional organization (i.e., body morphology, trophic guild, habitat preferences, and tolerance values). These functionally-similar groups were strongly correlated with independent hydrologic factors that differed significantly among the 34 sites. Fish assemblages defined in functional terms could thus be assigned to hydrologically variable sites (high flow variability, tendency to become seasonally intermittent) and hydrologically stable sites (low flow

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variability, high perennial baseflow). The stable sites could be further broken down into moderately stable and very stable sites. The functional organization of fish species in these two or three groups of sites followed theoretical expectations and provided strong support for the view that hydrologic factors are significant environmental variables that influence fish community structure. Several species of fish were identified as indicative of the variable-stable hydrologic gradient among stream sites.

The strong hydrologic-community relations found in the 34 WIMN sites suggest that hydrologic alterations induced by climatic change (or other anthropogenic disturbances) will modify stream fish assemblage structure in this region. These changes may be detected by evaluating the communities either in functional terms (e.g., generalists, tolerance) or in taxonomic terms. Shortcomings in the dataset (uneven sampling intensity across sites, variable periods of hydrologic record, etc.) suggest that our findings represent robust, general patterns of broad ecological interest. However, these same shortcomings caution against making firm predictions about specific biotic responses to climatic change until more reliable datasets have been evaluated.

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Figure 1. Map of all 816 sites used in the analysis showing distribution for a) states, b) hydrologic units, and c) ecoregions. Sites coded by "Δ" represent the 420 "best" sites, and sites coded by "$+$" indicate additional sites included in the complete 816-site analsysis (see Methods).

STATES / CLUS420 & CLUS816
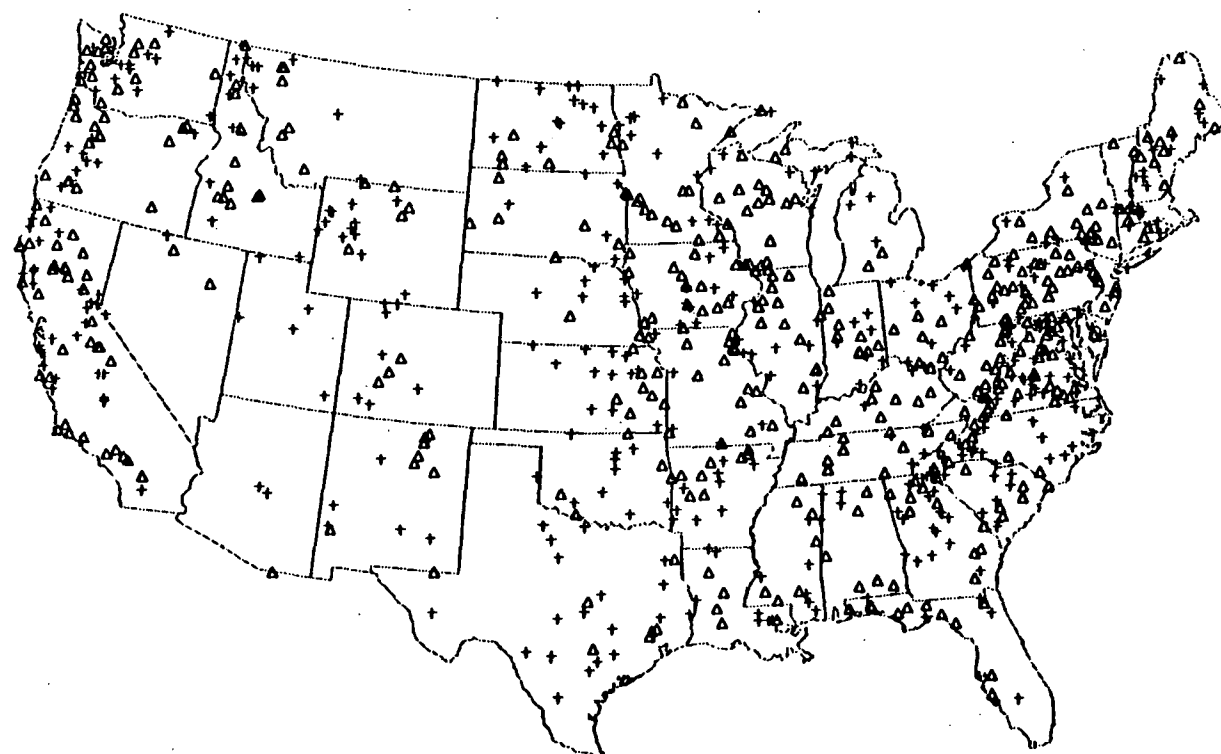
0 Miles 1000

△ CLUS420 POINTS
+ CLUS816 AND NOT "BEST"

HYDROLOGIC_UNITS / CLUS420 & CLUS816
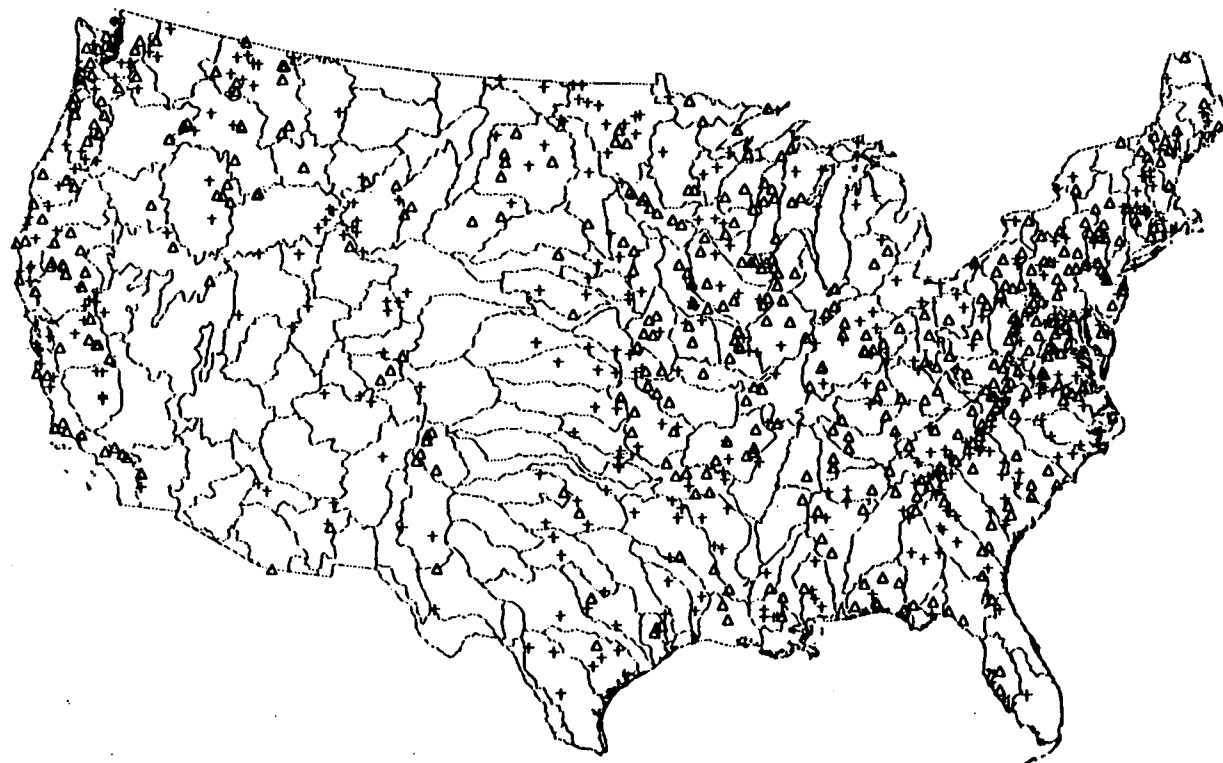
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+ CLUS816 AND NOT "BEST"

0   Miles   1000

ECOREGIONS / CLUS420 & CLUS816
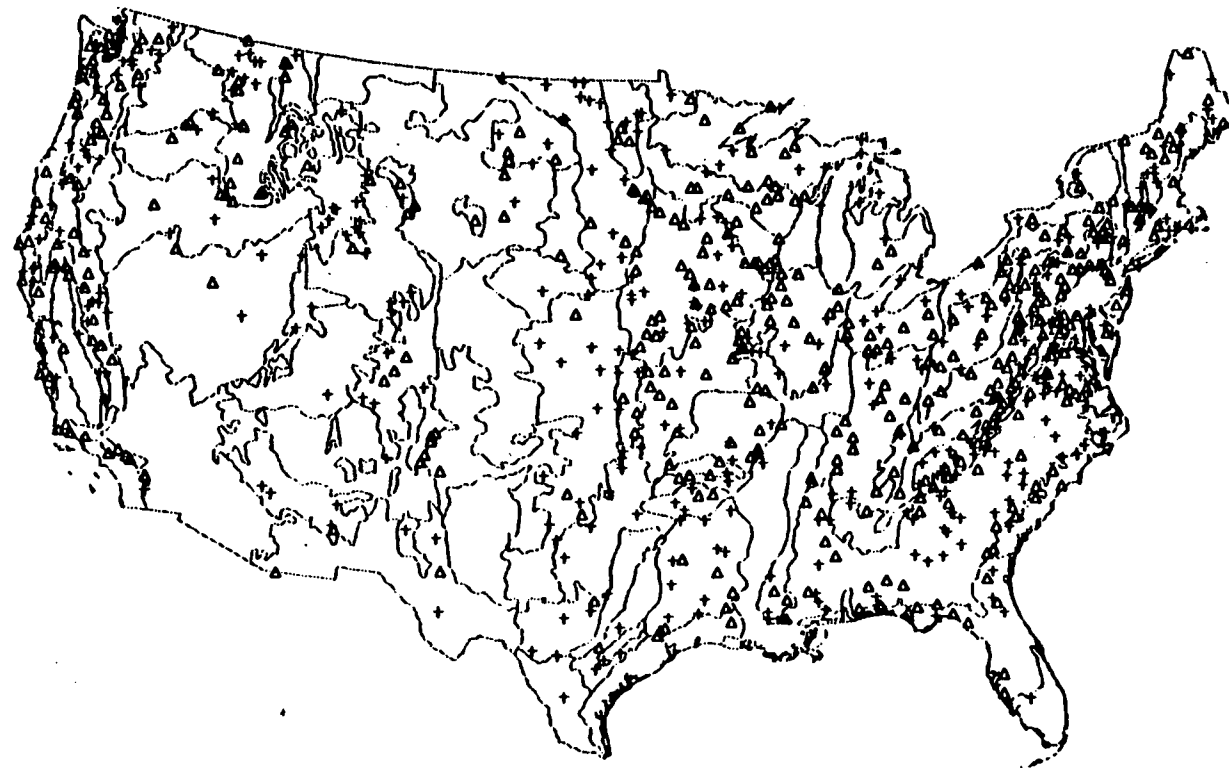
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+ CLUS816 AND NOT "BEST"
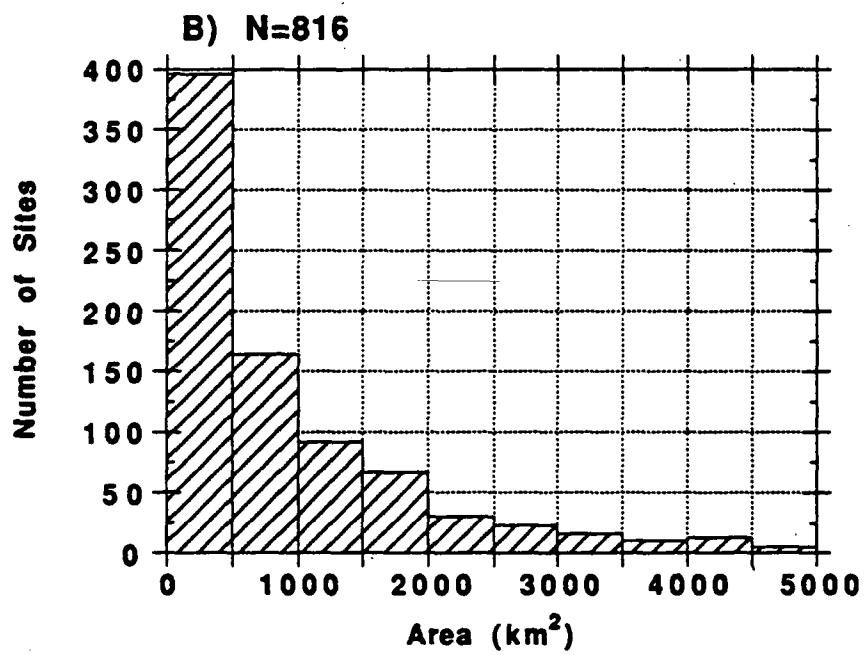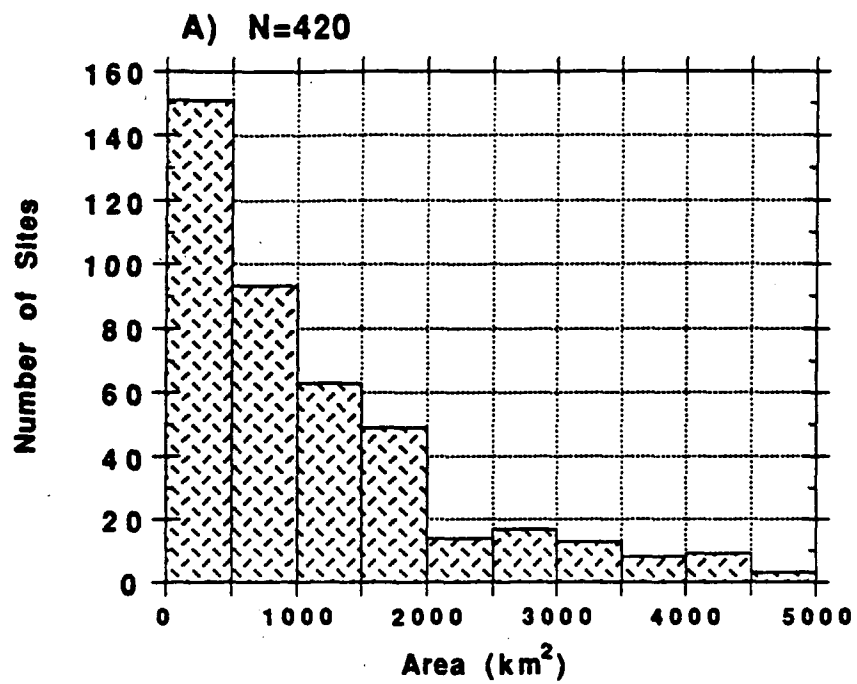
Figure 2. Histograms for catchment area for a) "best" sites and b) "all" sites.
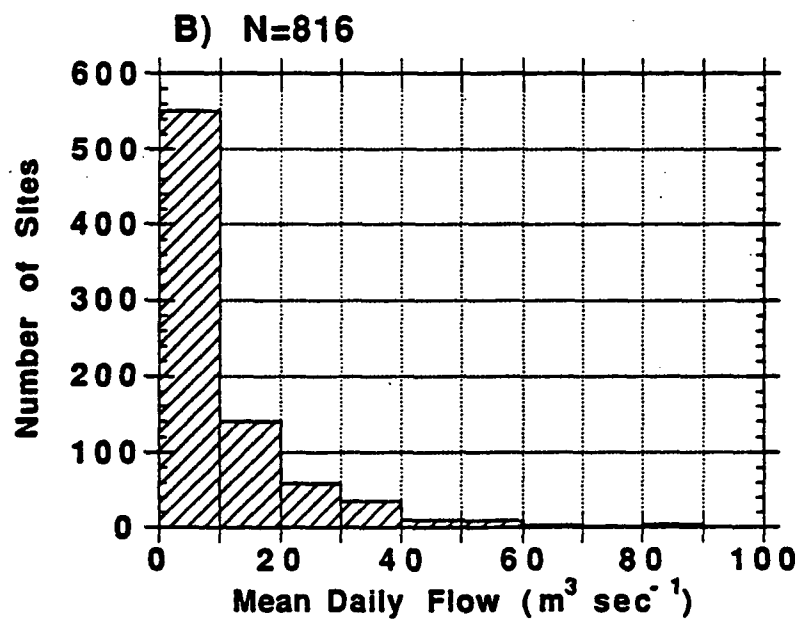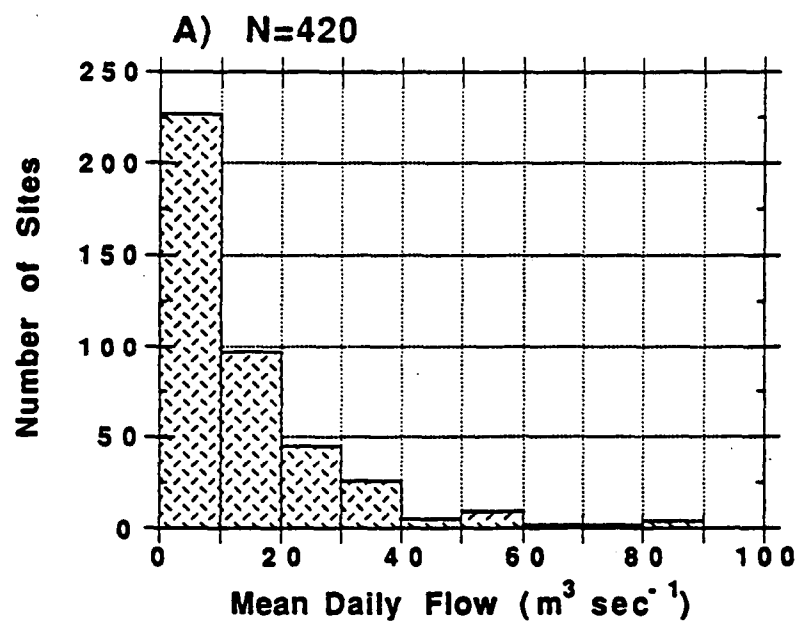
Figure 3. Histograms for mean daily flow (DAYAVE) for a) "best" sites and b) "all" sites.
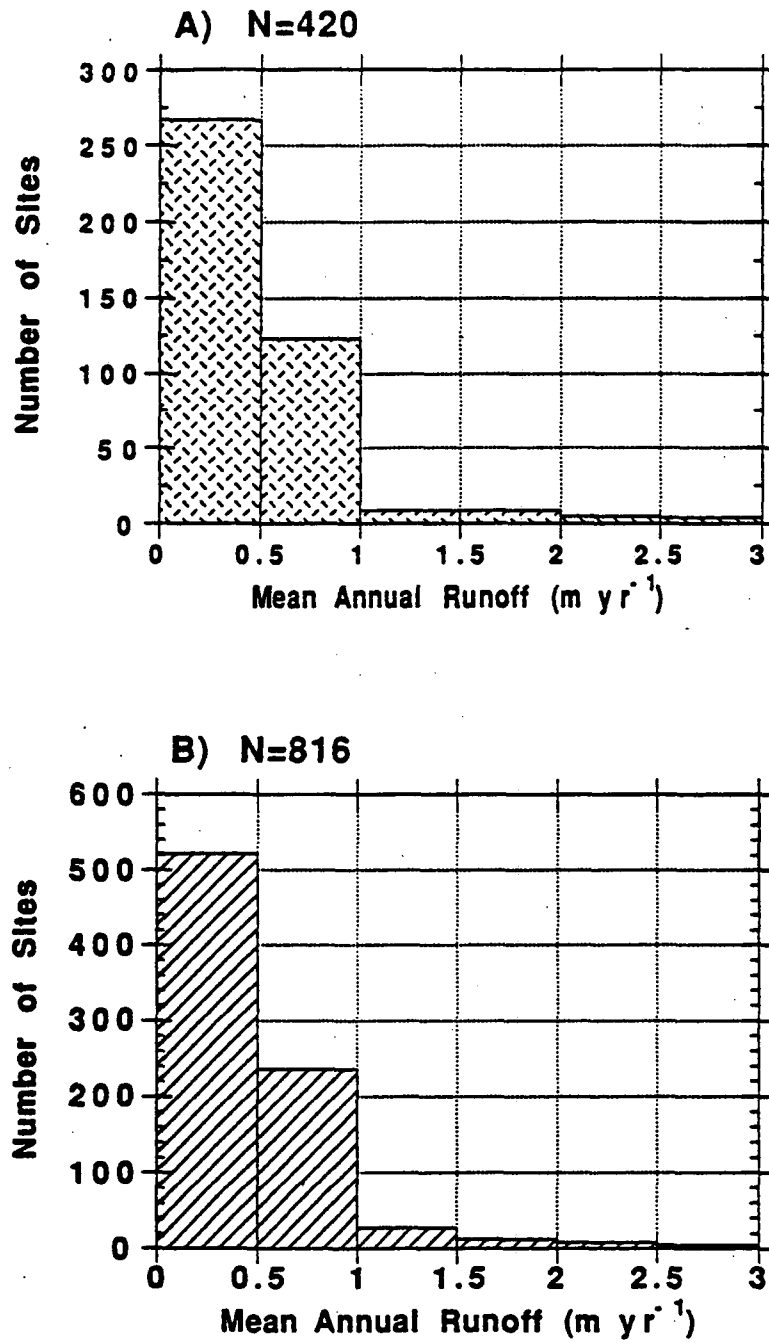
Figure 4. Histograms for mean annual runoff (MAR) for a) "best" sites and b) "all" sites.
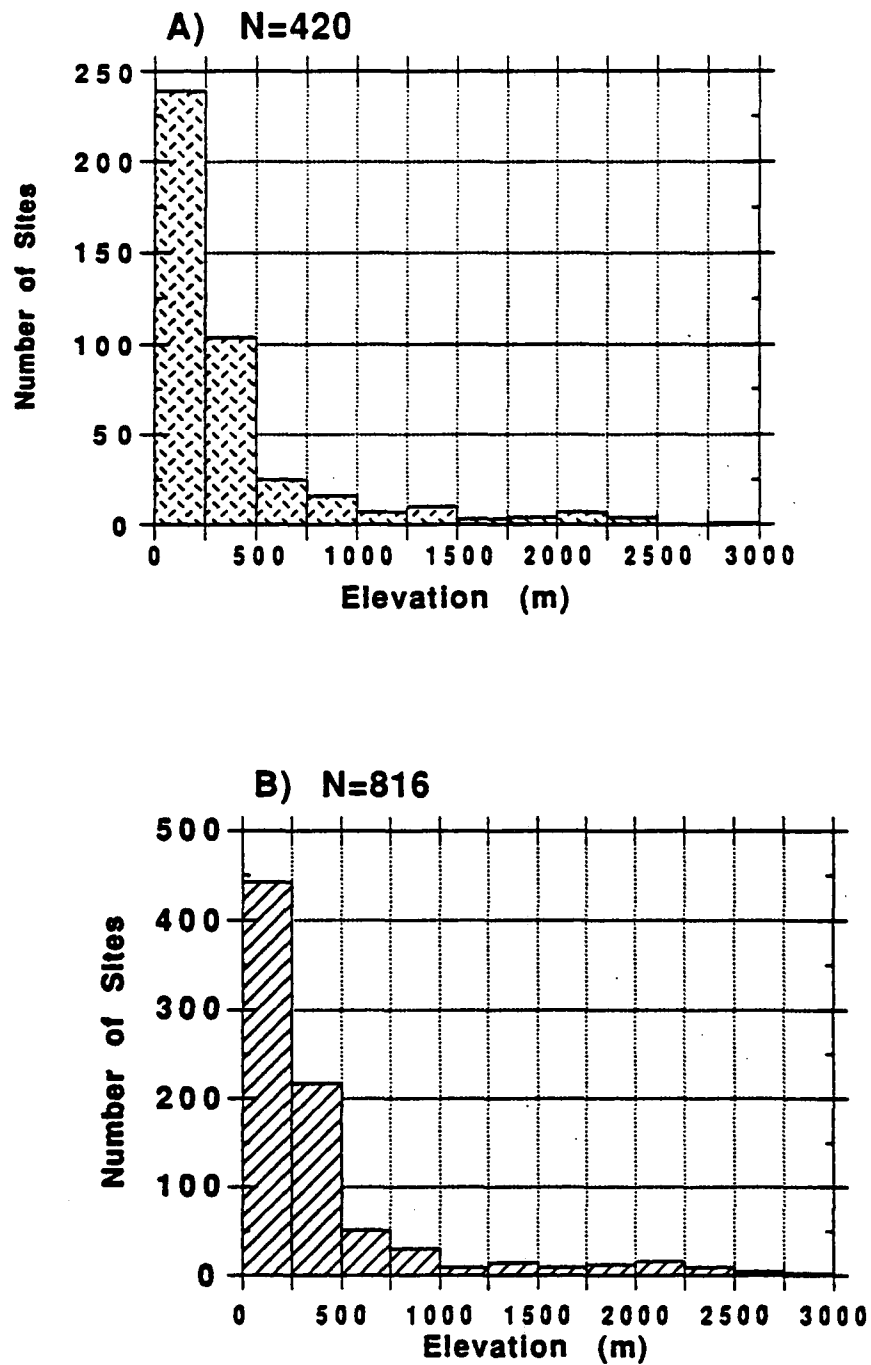
Figure 5. Histograms for stream gauge elevation for a) "best" sites and b) "all" sites. (Note: not all sites present due to some missing values.)
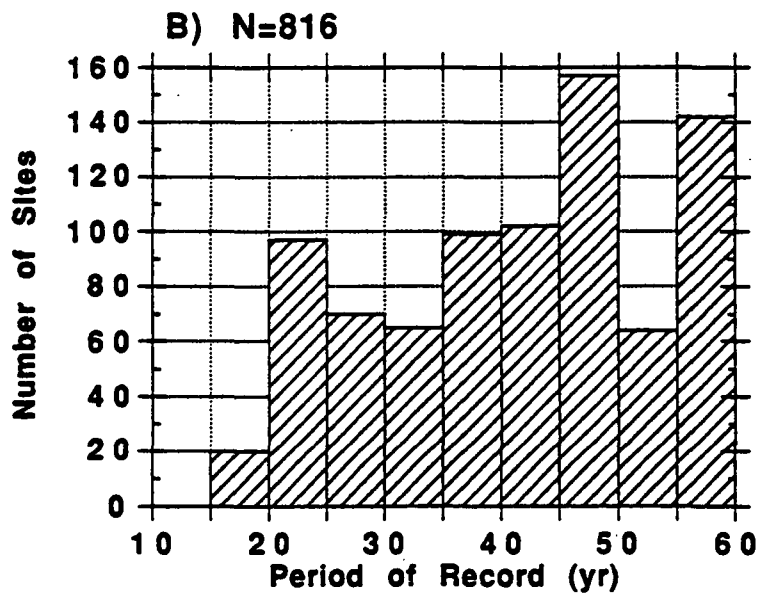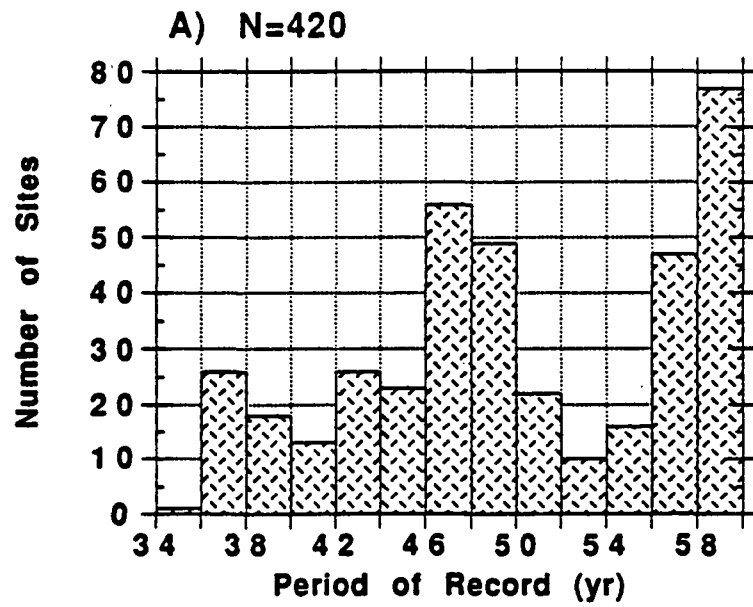
Figure 6. Histograms for period of record (POR) for a) "best" sites and b) "all" sites.
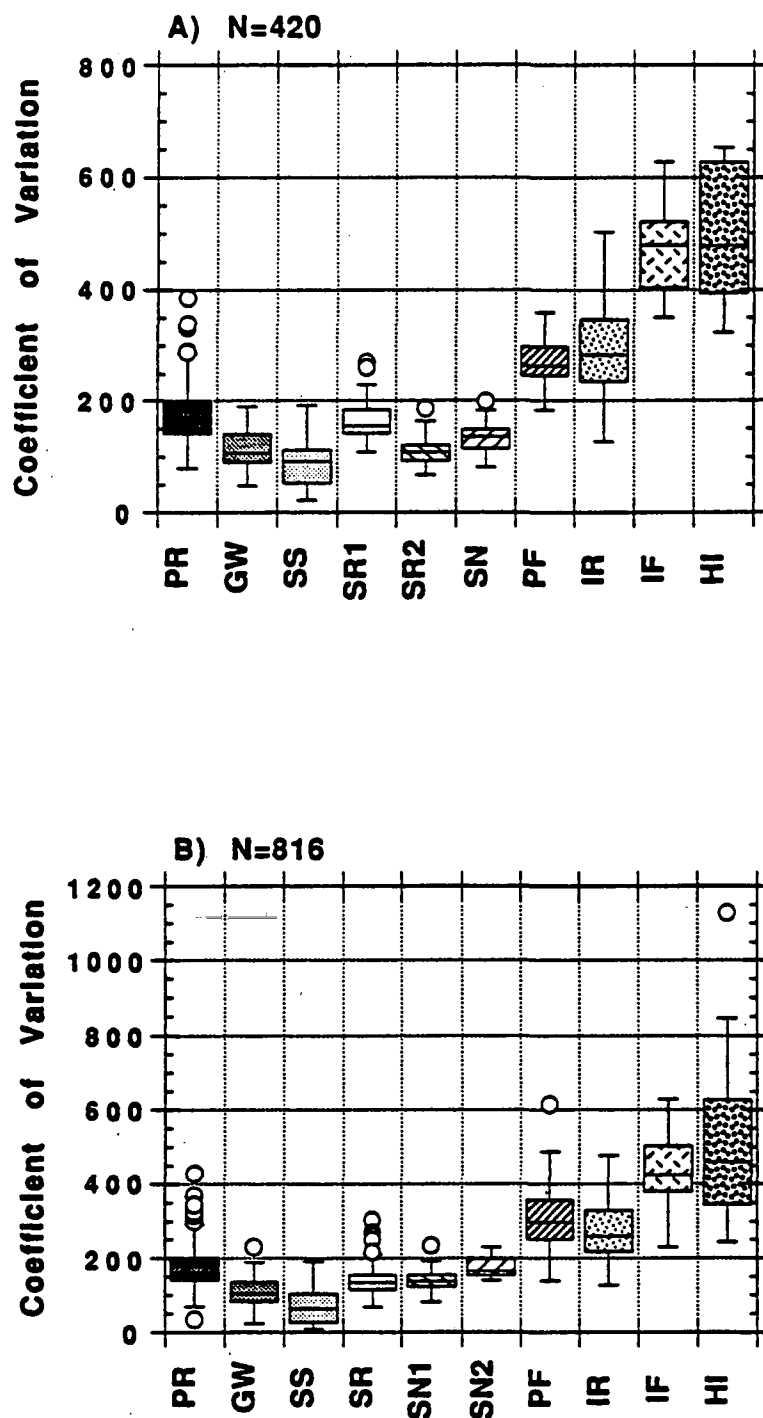
'Figure 7. Range of values for coefficient of variation for daily flow (DAYCV) for 10 clusters for a) "best" sites and b) "all" sites. Each box encloses 50% of observed values (median = horizontal line). Observed range is contained within upper and lower bars except for extreme outliers (circles). Stream type abbreviations are provided in Table 5.

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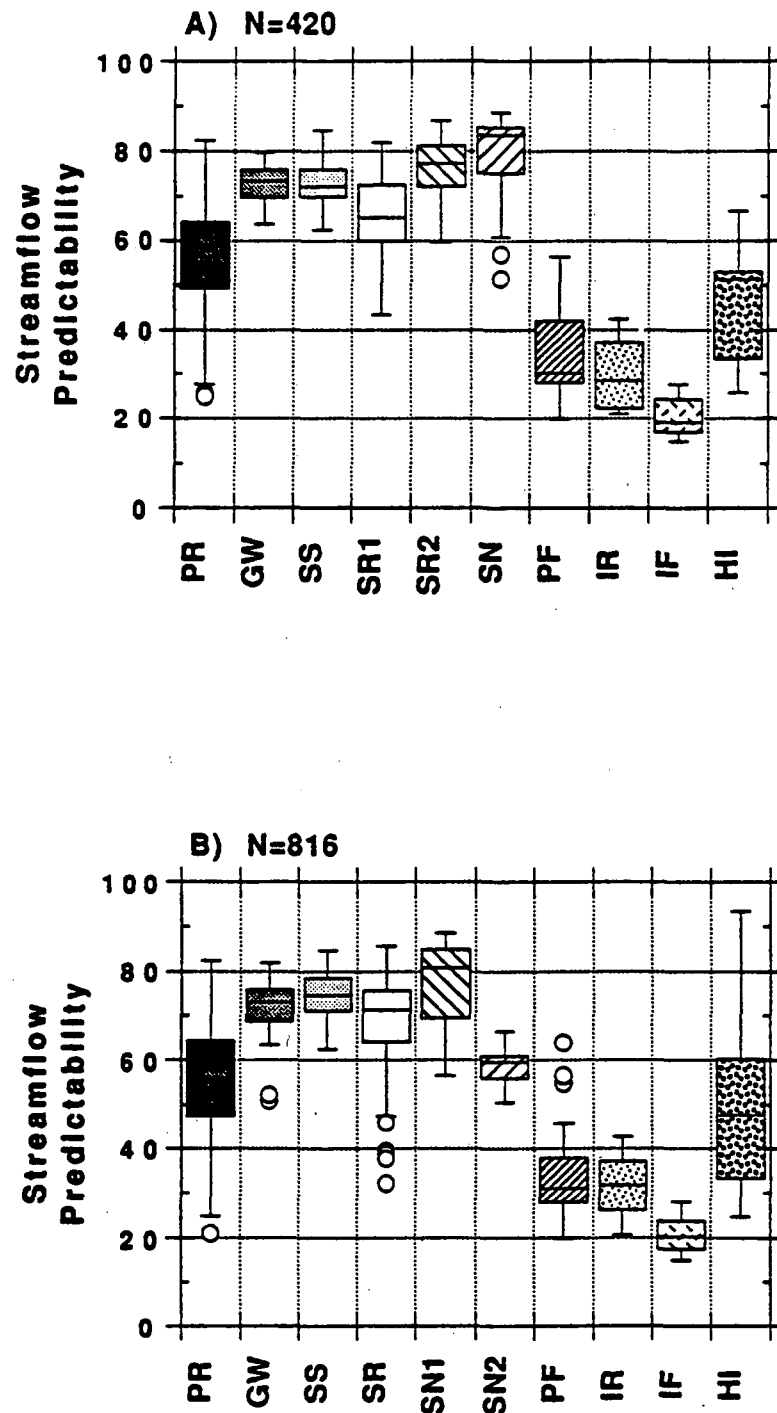
Figure 8. Range of values for Colwell's predictability of daily flow (DAYPRED) for 10 clusters for a) "best" sites and b) "all" sites. Symbols and abbreviations same as in Figure 7.
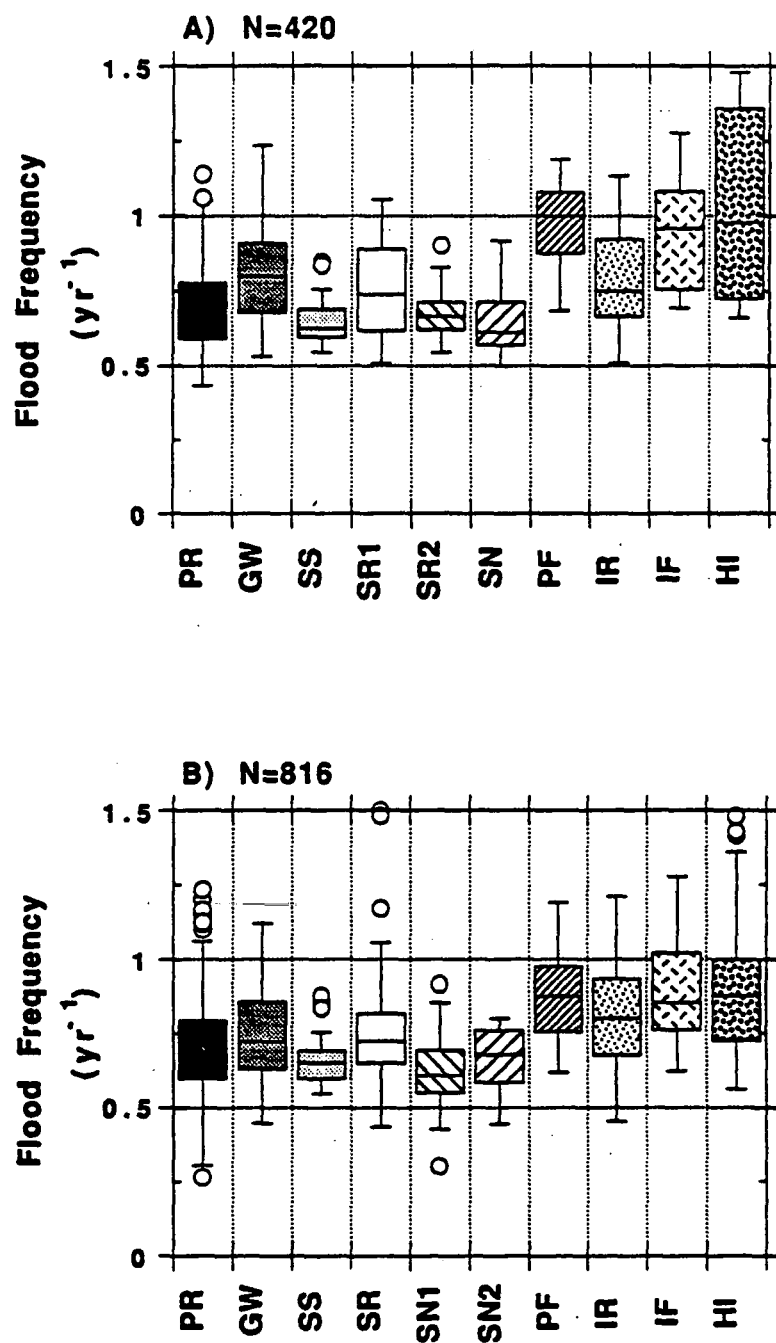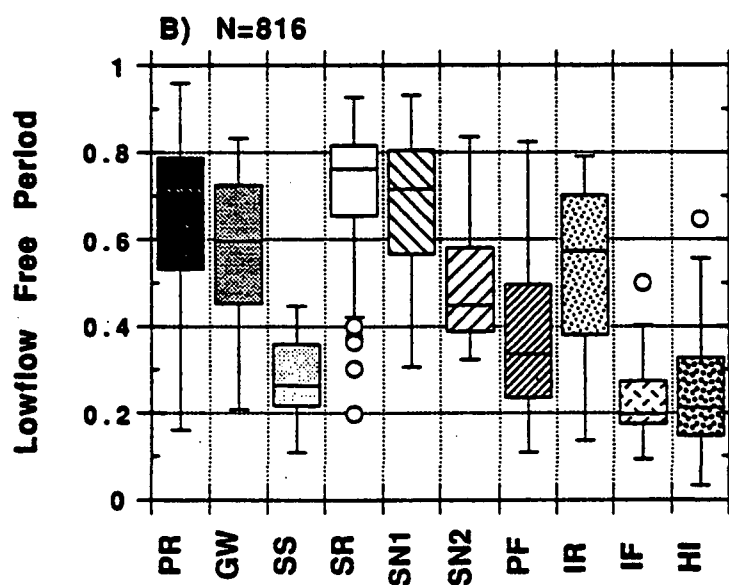
Figure 9. Range of values for flood frequency (FLODFREQ) for 10 clusters for a) "best" sites and b) "all" sites. Symbols and abbreviations same as in Figure 7.
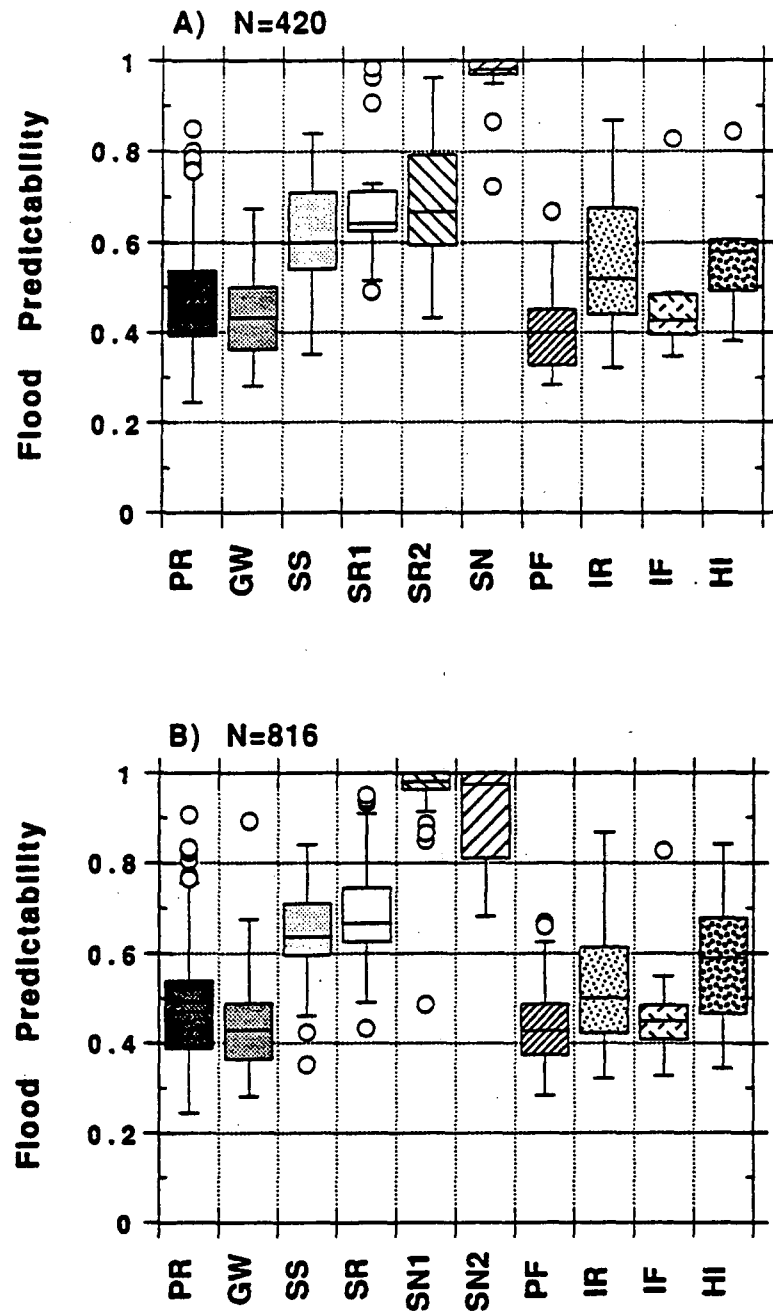
Figure 10. Range of values for flood predictability (FLODPRED) for 10 clusters for a) "best" sites and b) "all" sites. Symbols and abbreviations same as in Figure 7.
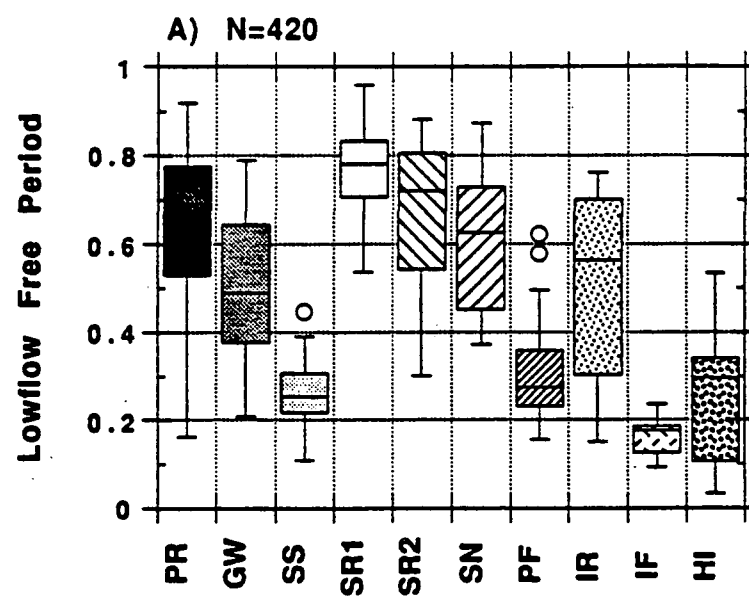
A) N=420

B) N=816
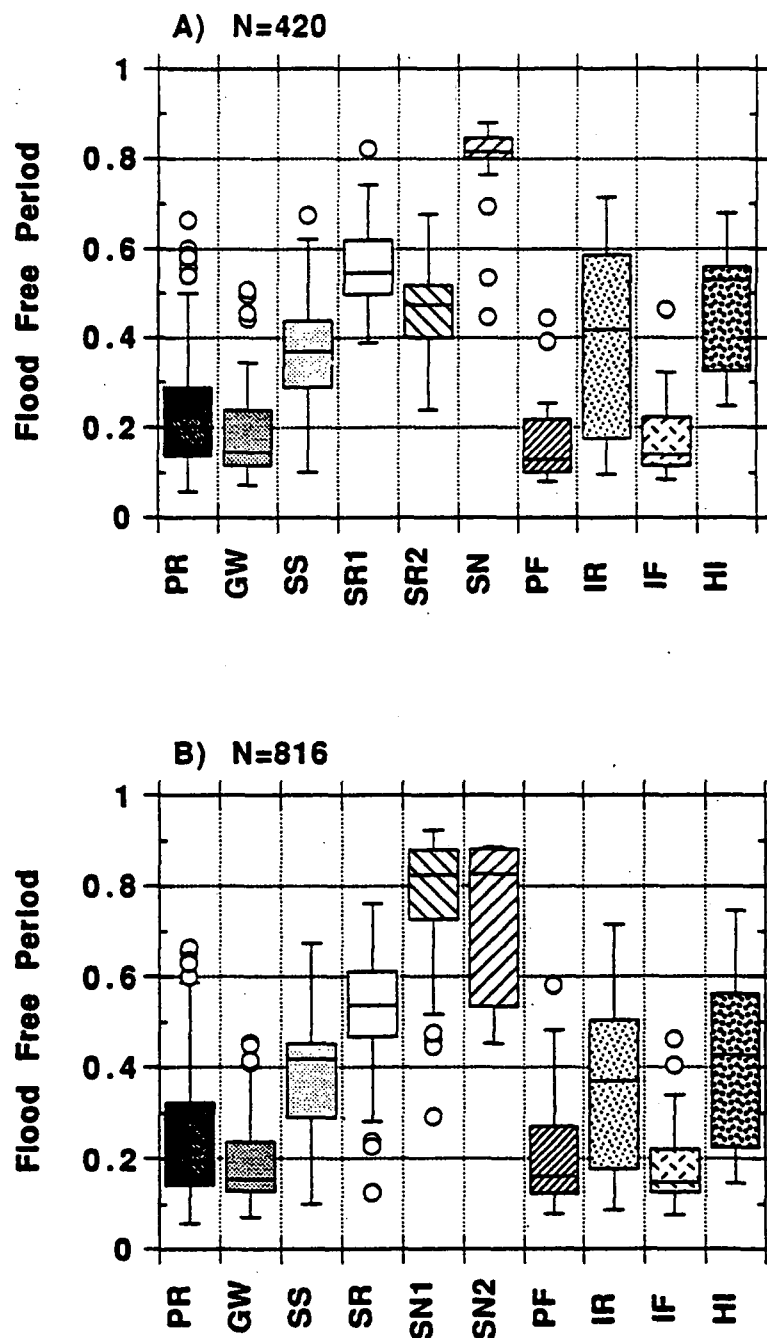
Figure 11. Range of values for flood-free period (FLODFREE) for 10 clusters for a) "best" sites and b) "all" sites. Symbols and abbreviations same as in Figure 7.
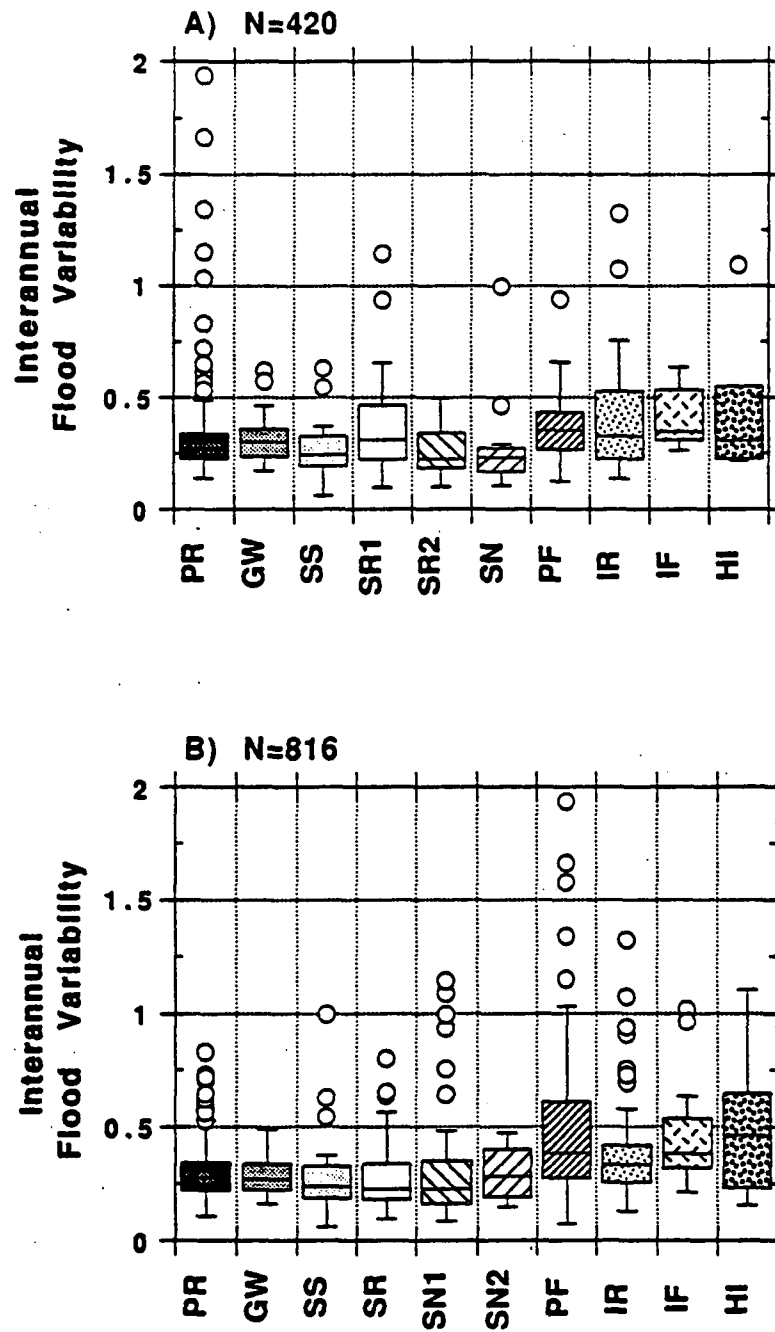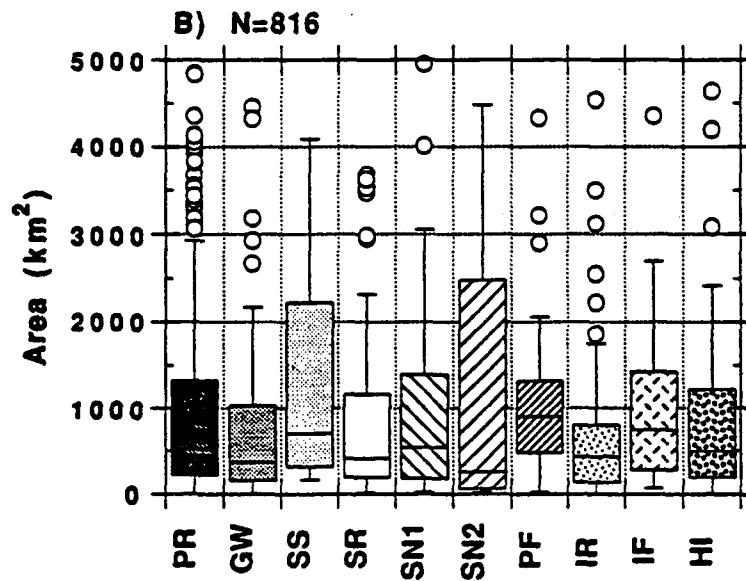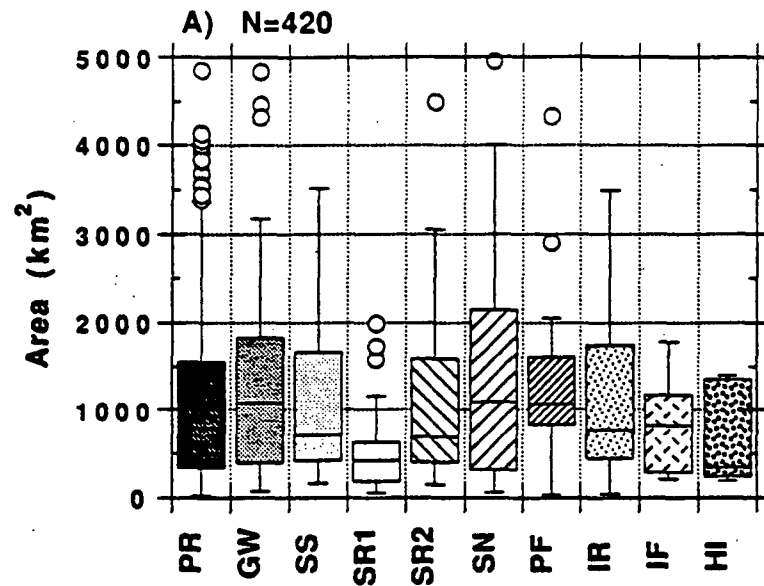
Figure 12. Range of values for interannual flood variability (FLODVAR) for 10 clusters for a) "best" sites and b) "all" sites. Symbols and abbreviations same as in Figure 7

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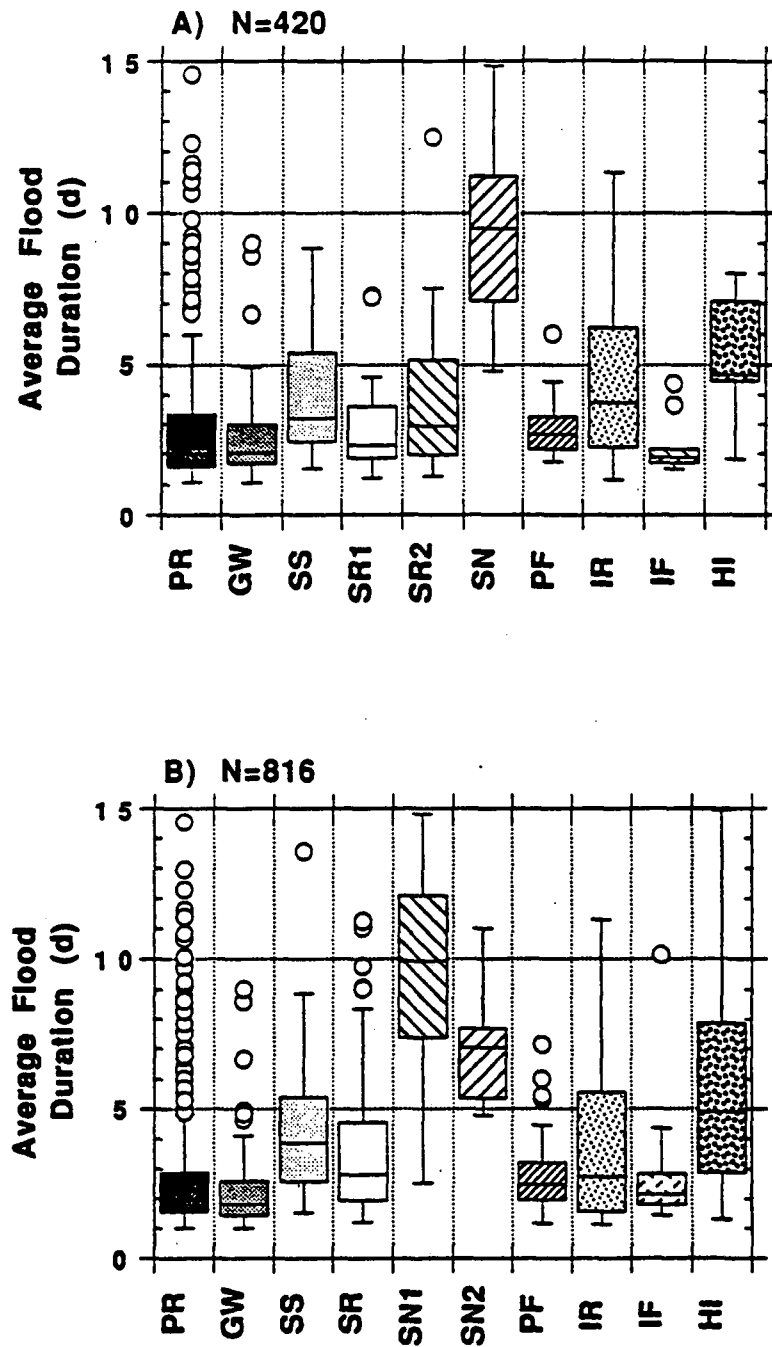
Figure 13. Range of values for average flood duration (FLODDUR) for 10 clusters for a) "best" sites and b) "all" sites. Symbols and abbreviations same as in Figure 7.
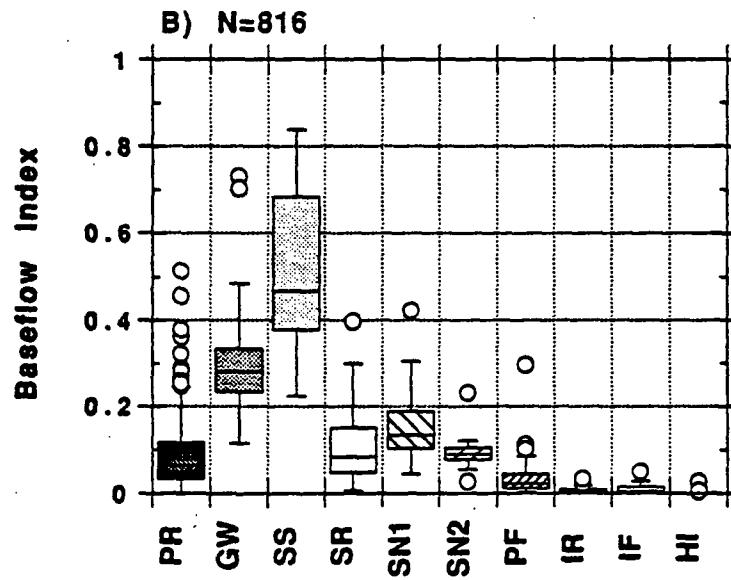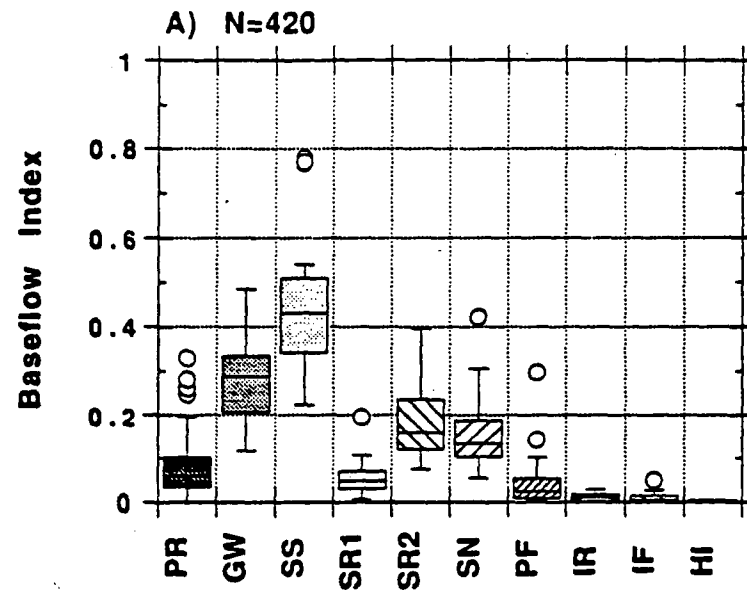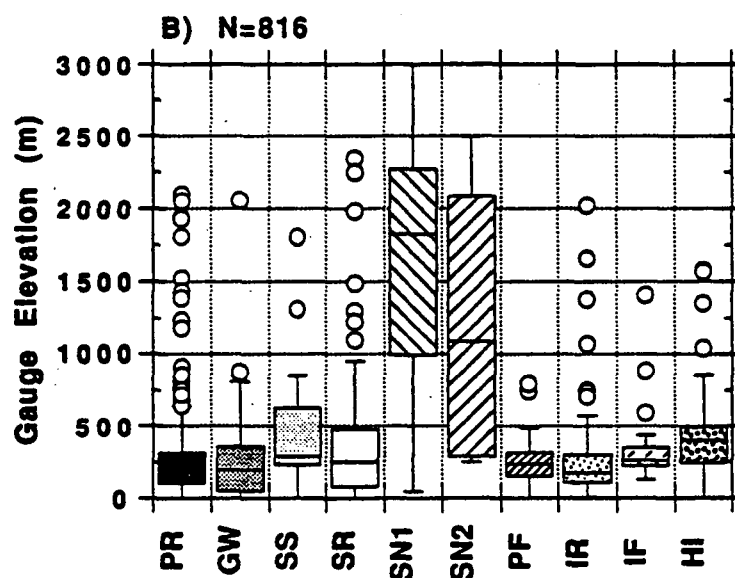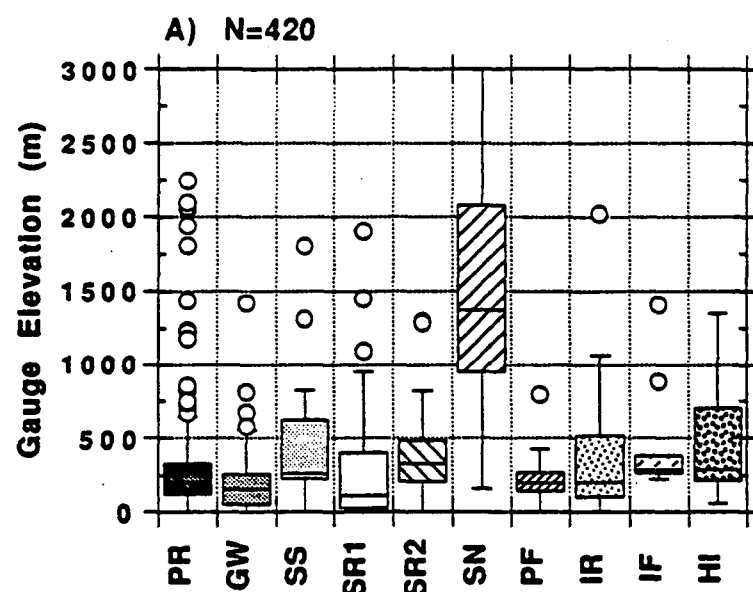
Figure 14. Range of values for baseflow index (BFI) for 10 clusters for a) "best" sites and b) "all" sites. Symbols and abbreviations same as in Figure 7.
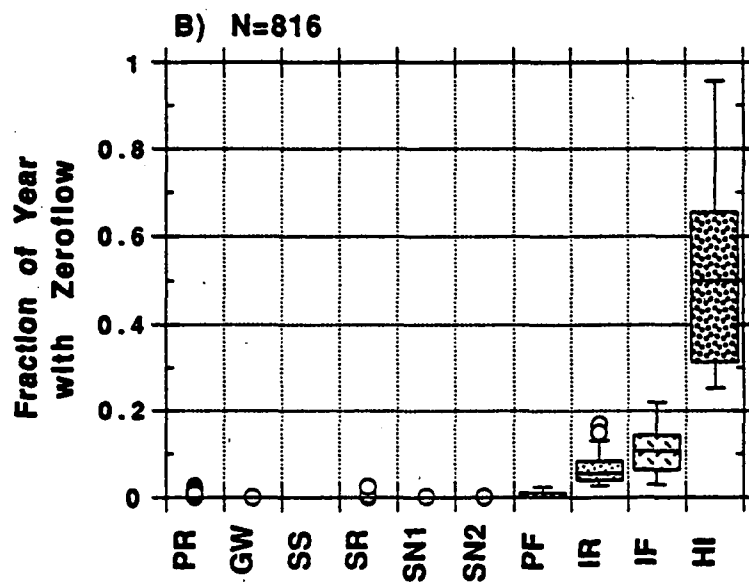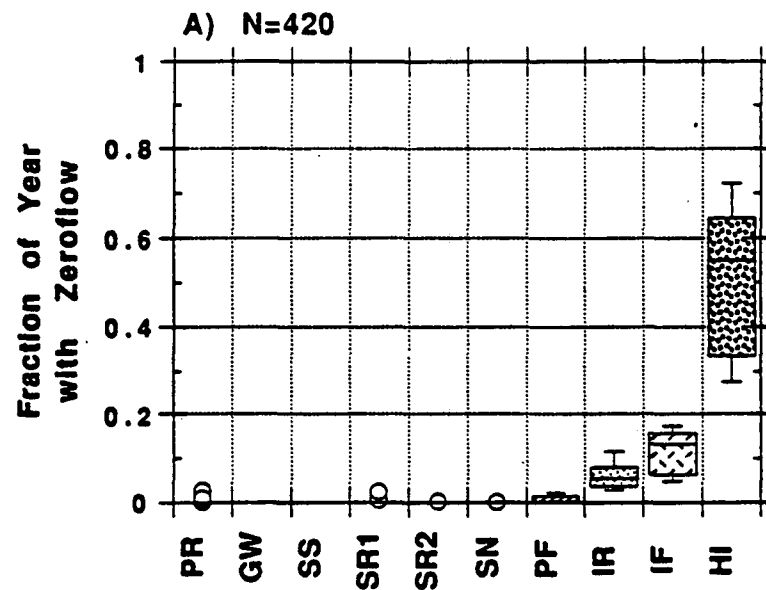
Figure 15. Range of values for average period of zero flow (ZERODAY) for 10 clusters for a) "best" sites and b) "all" sites. Symbols and abbreviations same as in Figure 7.
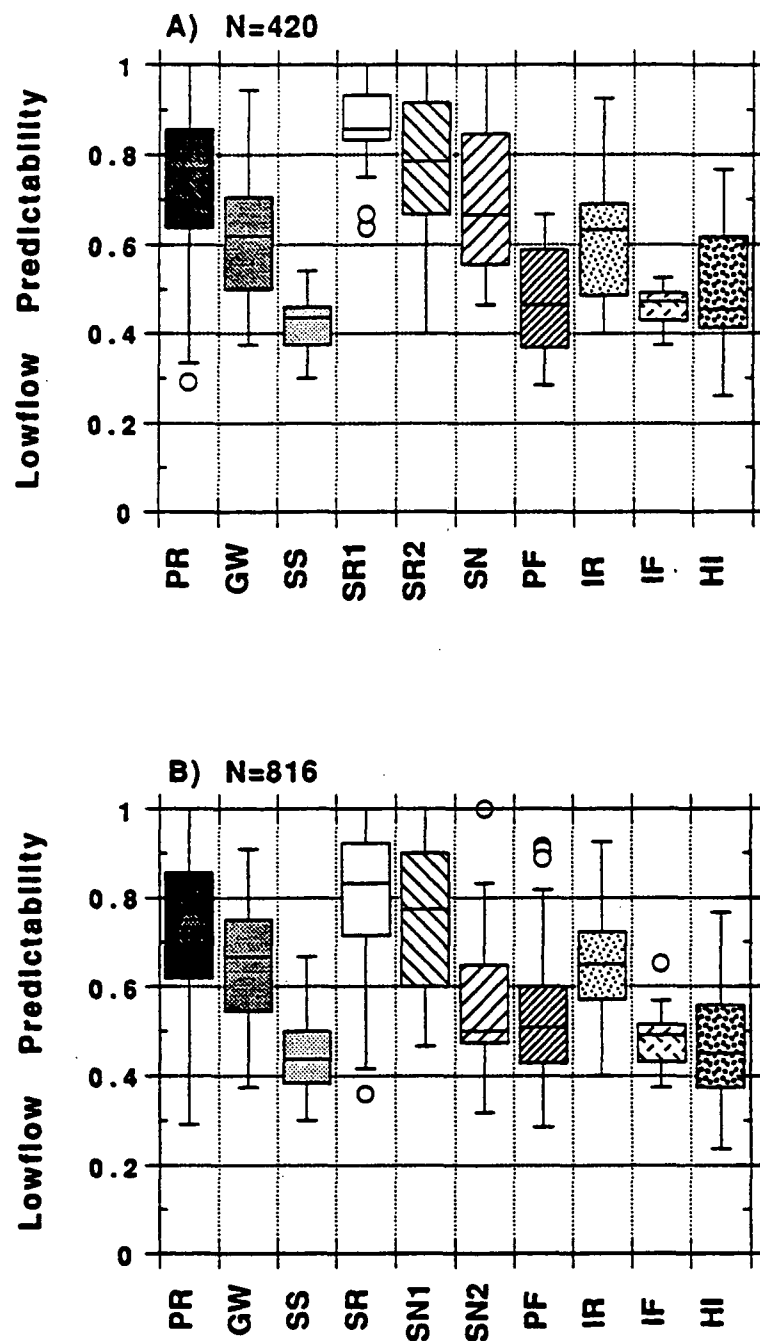
Figure 16. Range of values for lowflow predictability (LOWPRED) for 10 clusters for a) "best" sites and b) "all" sites. Symbols and abbreviations same as in Figure 7.

Figure 17. Range of values for lowflow-free period (LOWFREE) for 10 clusters for a) "best" sites and b) "all" sites. Symbols and abbreviations same as in Figure 7.
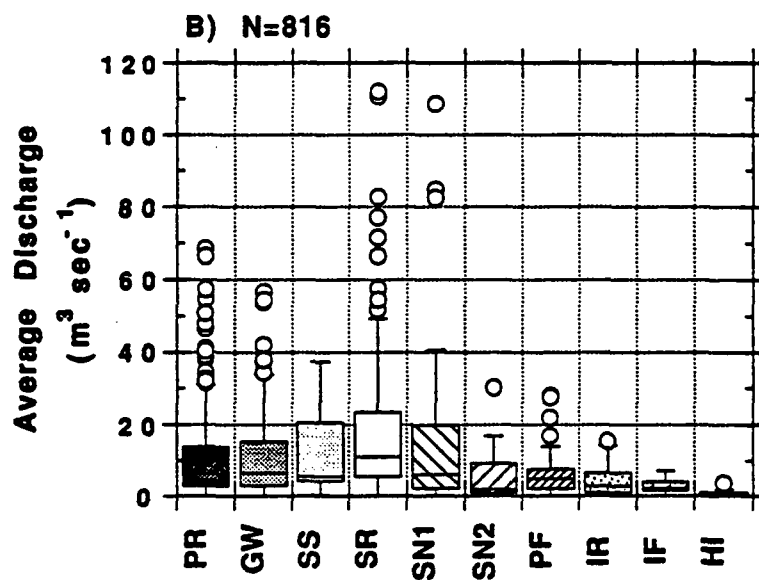
Figure 18. Range of values for catchment area (AREA) for 10 clusters for a) "best" sites and b) "all" sites. Symbols and abbreviations same as in Figure 7.
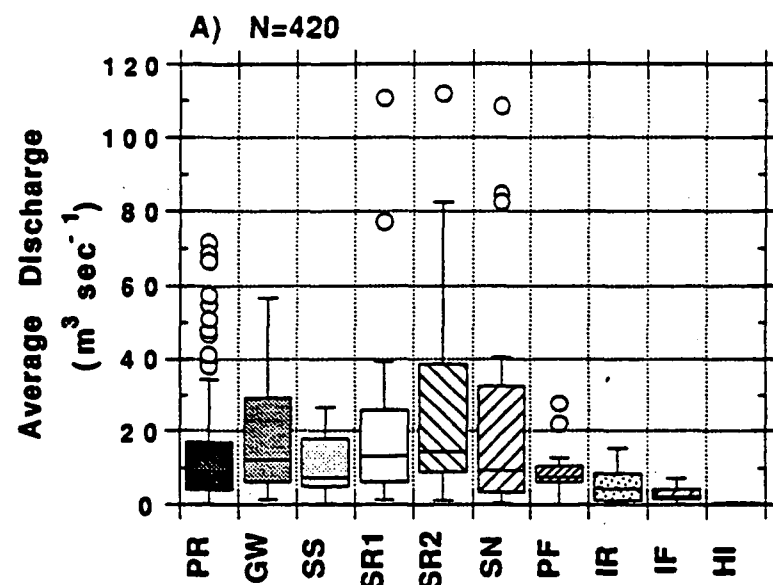
Figure 19. Range of values for gauge elevation (ELEV) for 10 clusters for a) "best" sites and b) "all" sites. Symbols and abbreviations same as in Figure 7.

Figure 20. Range of values for average daily flow (DAYAVE) for 10 clusters for
a) "best" sites and b) "all" sites. Symbols and abbreviations same as
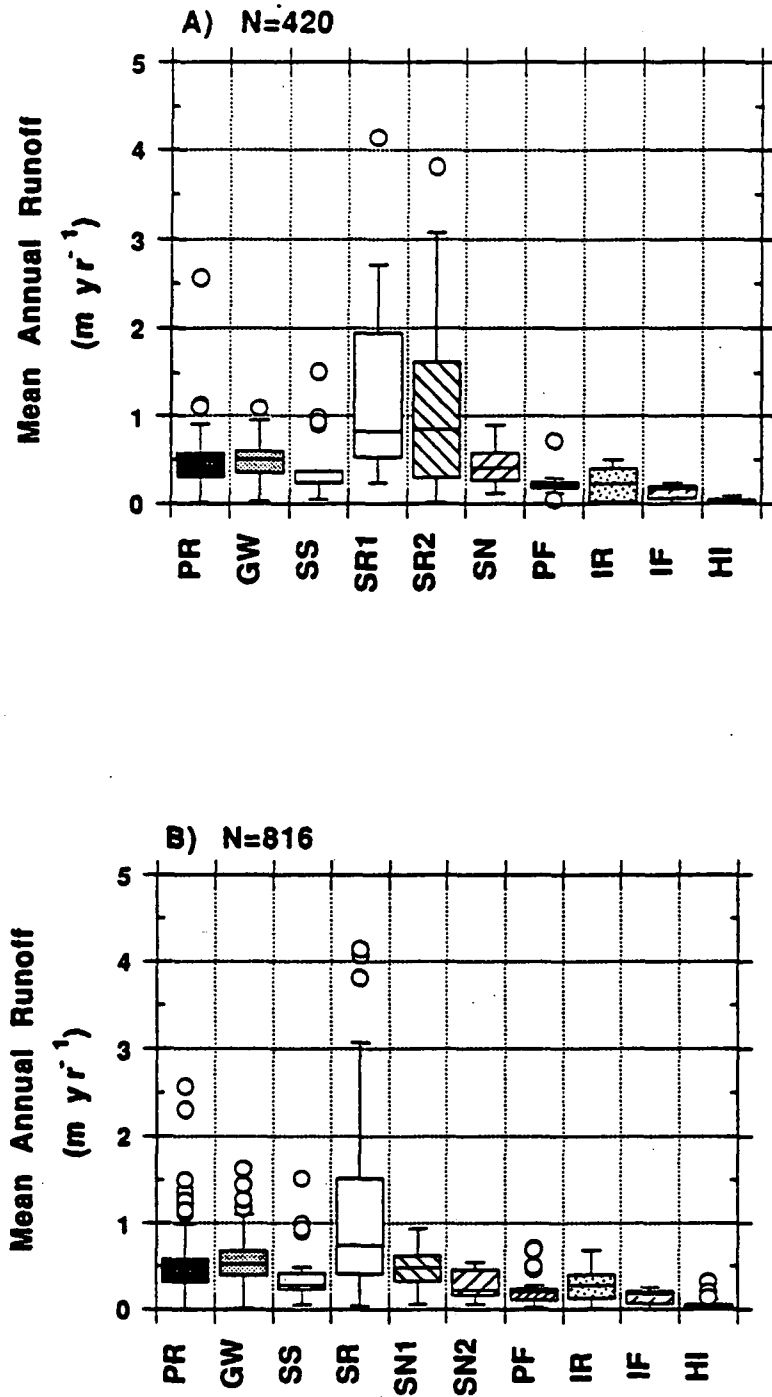in Figure 7.

Figure 21. Range of values for mean annual runoff (MAR) for 10 clusters for a) "best" sites and b) "all" sites. Symbols and abbreviations same as in Figure 7.
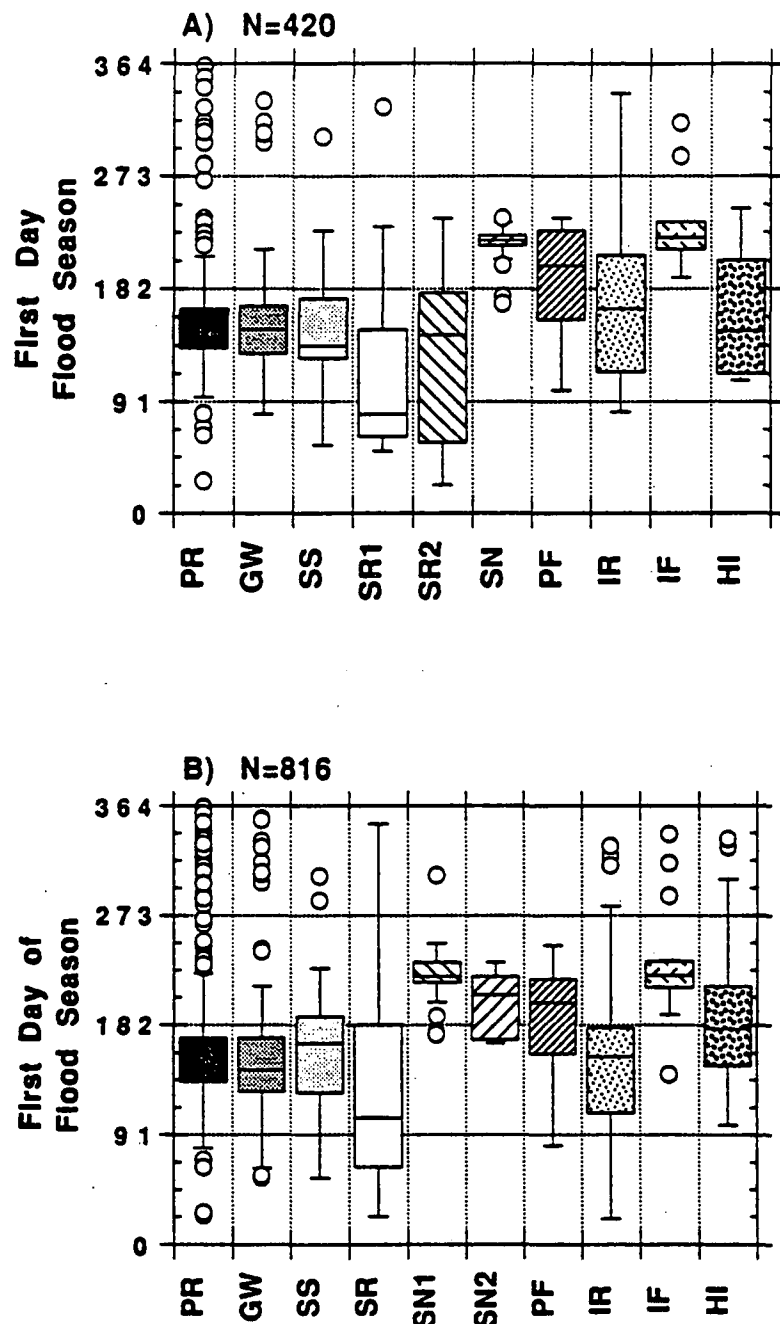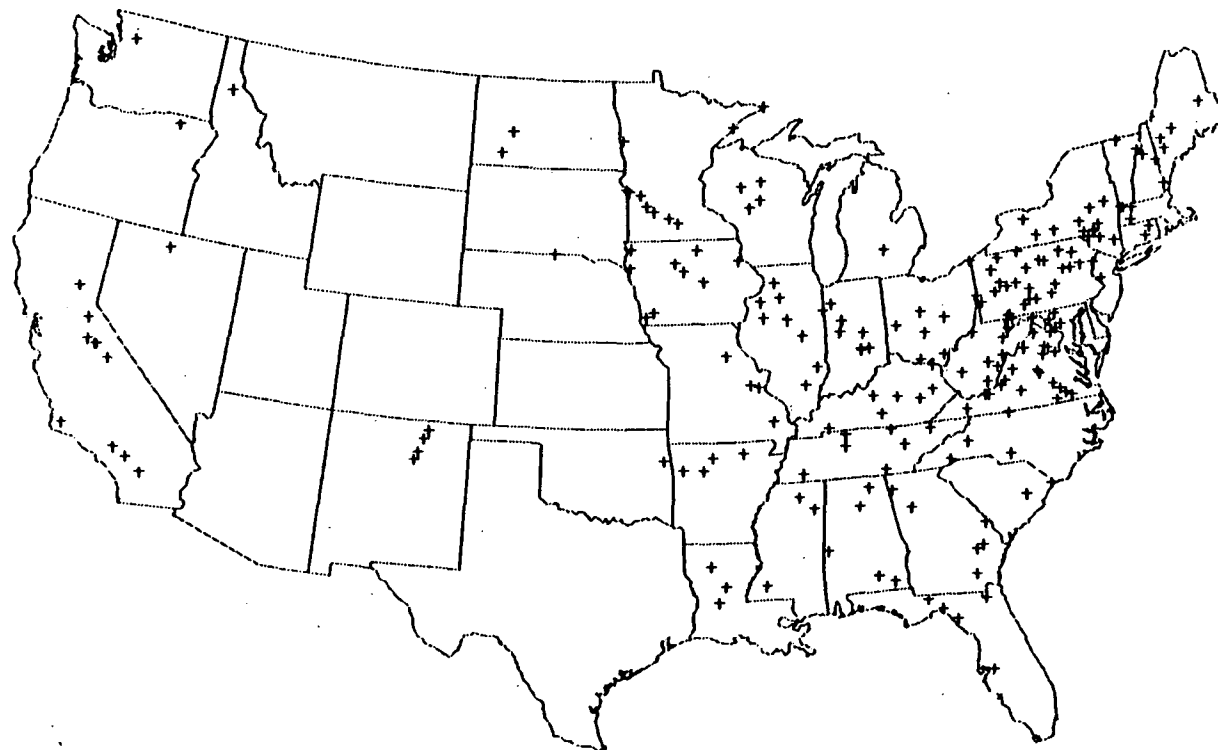
Figure 22. Range of values for first day of the flood period (FLODTIME) for 10 clusters for a) "best" sites and b) "all" sites. Symbols and abbreviations same as in Figure 7.

Figure 23. Maps showing geographical distribution of 420 "best" sites for a) Perennial Runoff (PR), b) GW (Stable Groundwater), c) SS (Superstable Groundwater), d) Snow+Rain (SR1 and SR2), e) Snowmelt (SN), f) Perennial Flashy (PF), and g) Intermittent Runoff (IR), Intermittent Flashy (IF), and Harsh Intermittent (HI) streams.
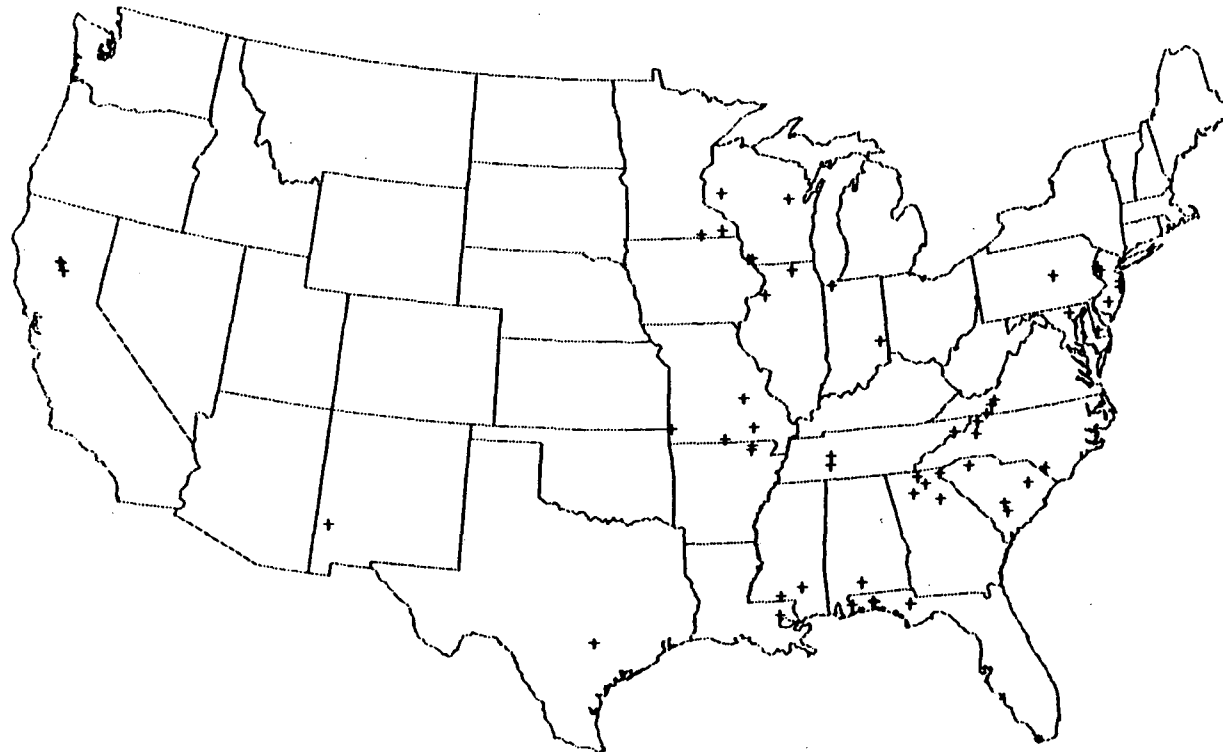
STATES / CLUS420 / 'PR'

+ CLUS420 : CLUSNAME = 'PR' -> 209 of 420

0   Miles   1000

STATES / CLUS420 / 'GW'

+ CLUS420 : CLUSNAME = 'GW' -> 55 of 420

0   Miles   1000

STATES / CLUS420 / 'SS'

+ CLUS420 : CLUSNAME = 'SS' -> 17 of 420

0   Miles   1000

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STATES / CLUS420 / ,'SR1','SR2'
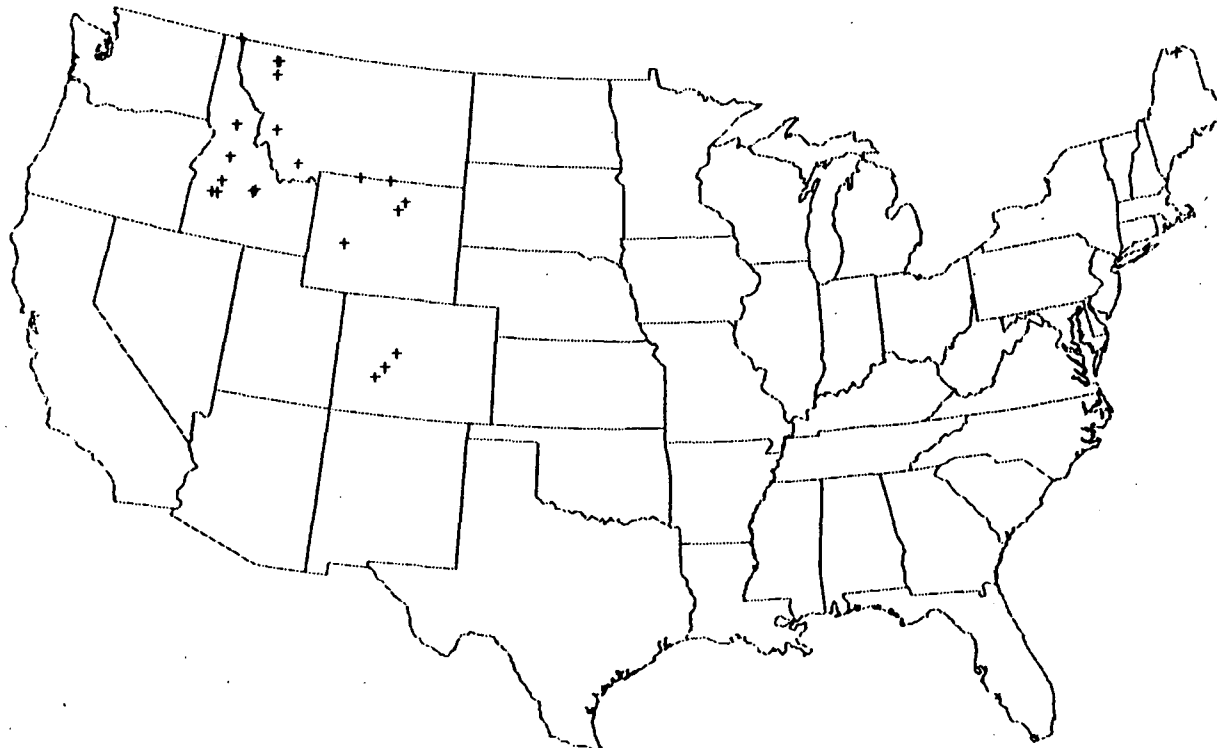
+ CLUS420 : CLUSNAME = 'SR1' -> 27 of 420
△ CLUS420 : CLUSNAME = 'SR2' -> 29 of 420

0   Miles   1000

STATES / CLUS420 / 'SN'

+ CLUS420 : CLUSNAME = 'SN' -> 22 of 420

0   **Miles**   1000

STATES / CLUS420 / 'PF'

+ CLUS420 : CLUSNAME = 'PF' -> 24 of 420

0   Miles   1000

STATES / CLUS420 / ,'IR','IF','HI'
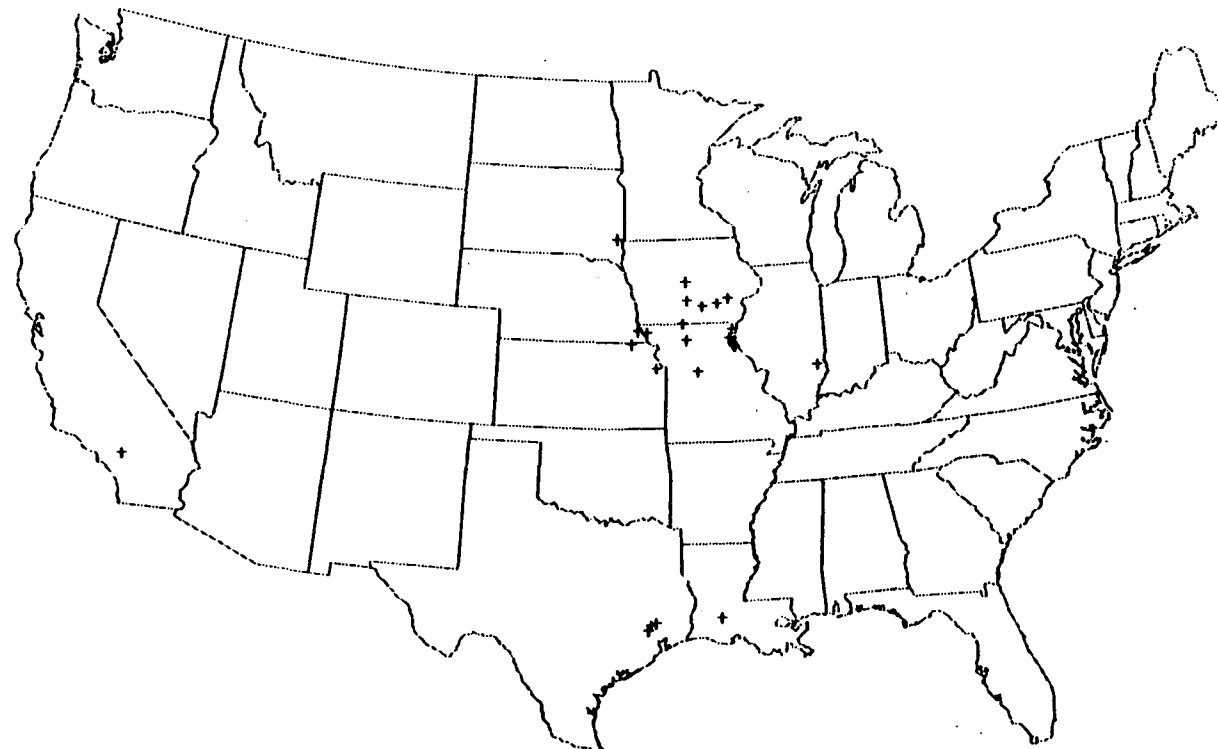
0   **Miles**   1000

+	CLUS420 : CLUSNAME = 'IR' -> 20 of 420
△	CLUS420 : CLUSNAME = 'IF' -> 10 of 420
◇	CLUS420 : CLUSNAME = 'HI' -> 7 of 420

Figure 24. Maps showing geographical distribution of "all" 816 sites for a) Perennial Runoff (PR), b) GW (Stable Groundwater), c) SS (Superstable Groundwater), d) Snow+Rain , e) Snowmelt (SN1 and SN2), f) Perennial Flashy (PF), and g) Intermittent Runoff (IR), Intermittent Flashy (IF), and Harsh Intermittent (HI) streams.

STATES / CLUS816 / 'PR'
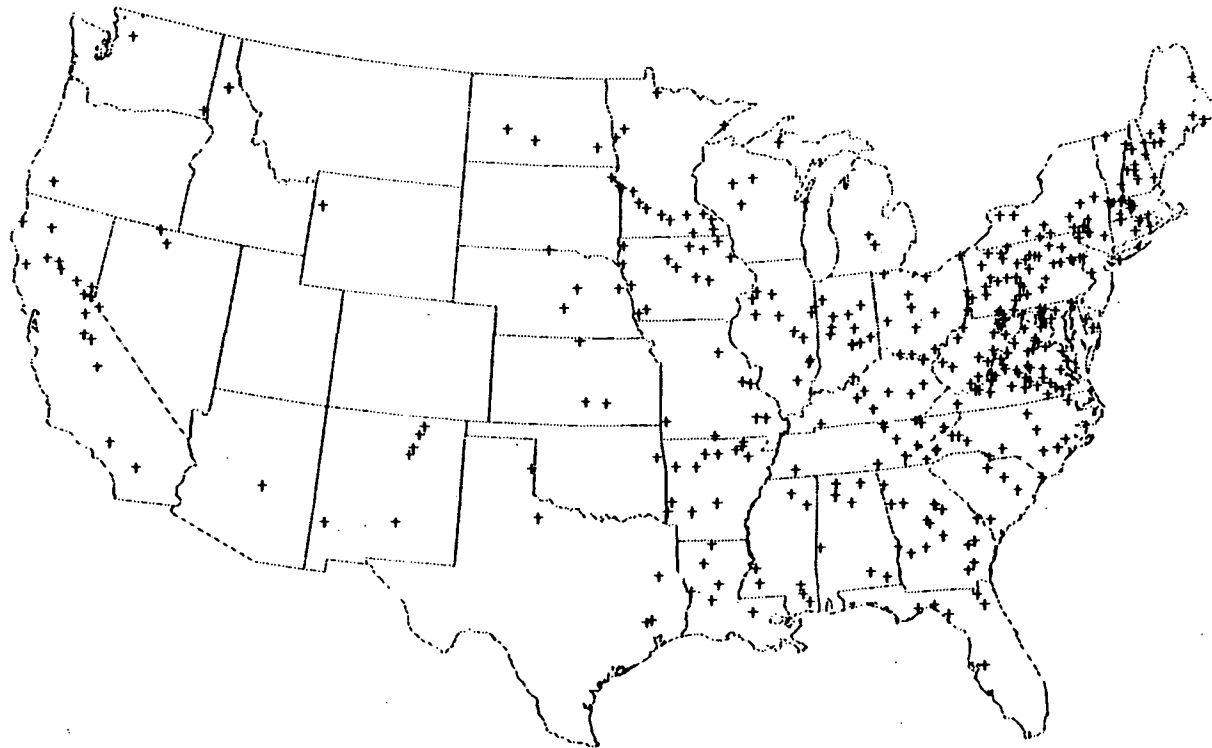
+ CLUS816 : CLUSNAME = 'PR' -> 384 of 816
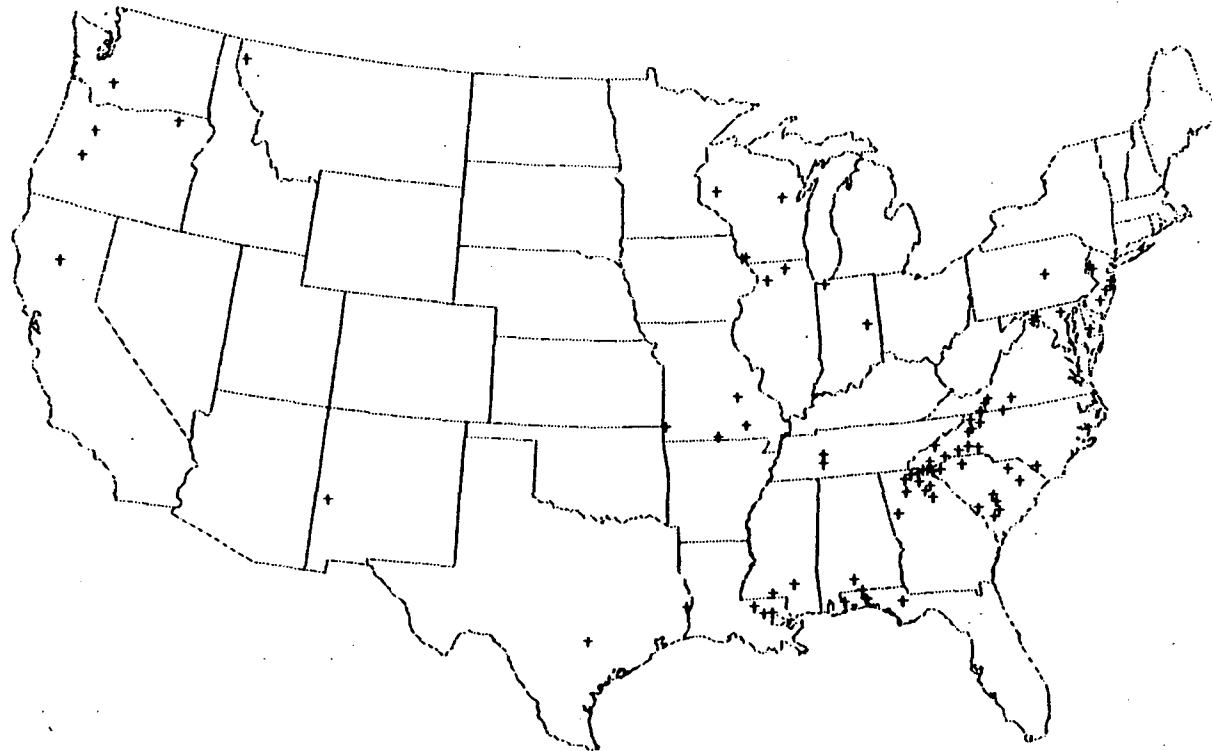
0   Miles   1000

STATES / CLUS816 / 'GW'

+ CLUS816 : CLUSNAME = 'GW' -> 84 of 816
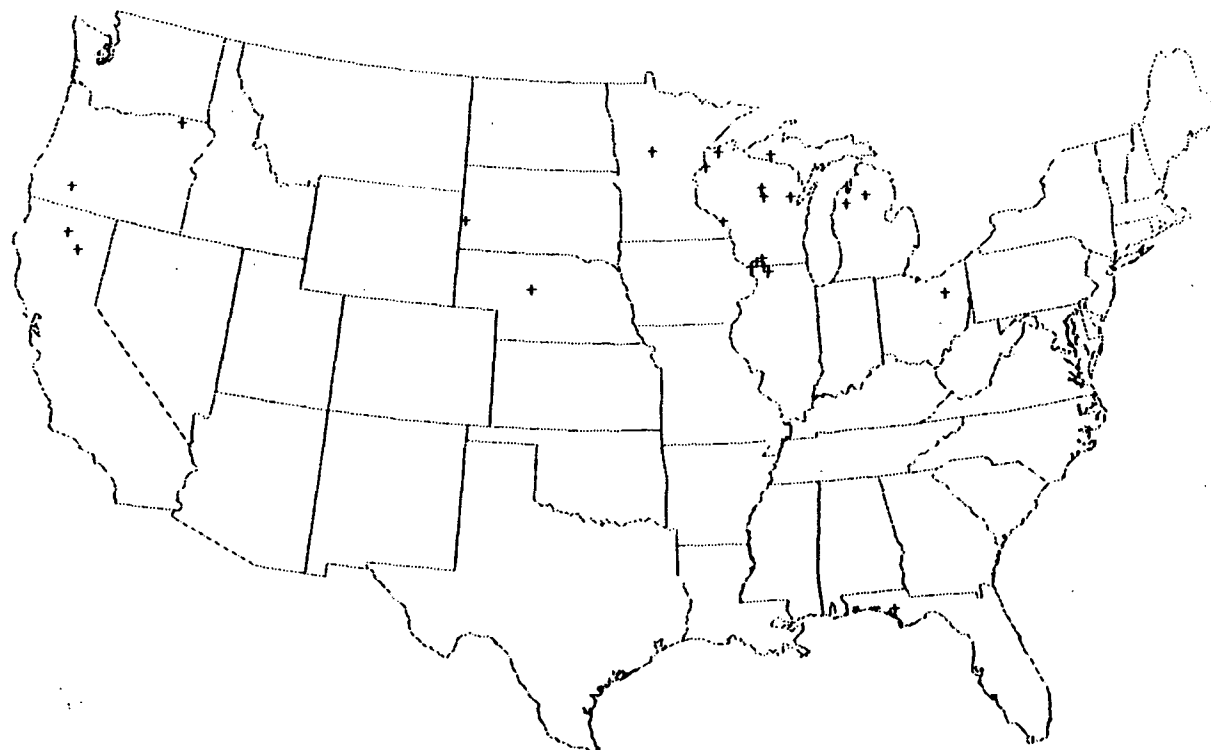
0   Miles   1000

STATES / CLUS816 / 'SS'

+ CLUS816 : CLUSNAME = 'SS' -> 23 of 816
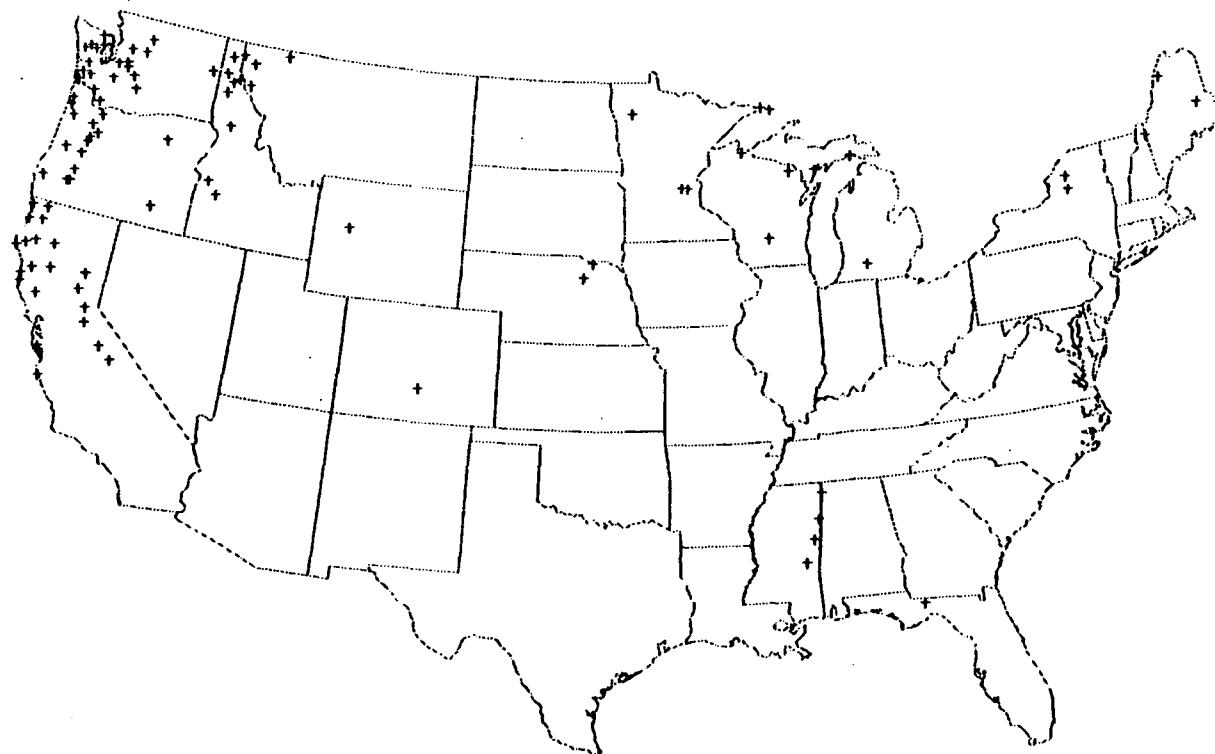
0   Miles   1000

STATES / CLUS816 / 'SR'

⁺ CLUS816 : CLUSNAME = 'SR' -> 101 of 816

0   Miles   1000

STATES / CLUS816 / ,'SN1','SN2'
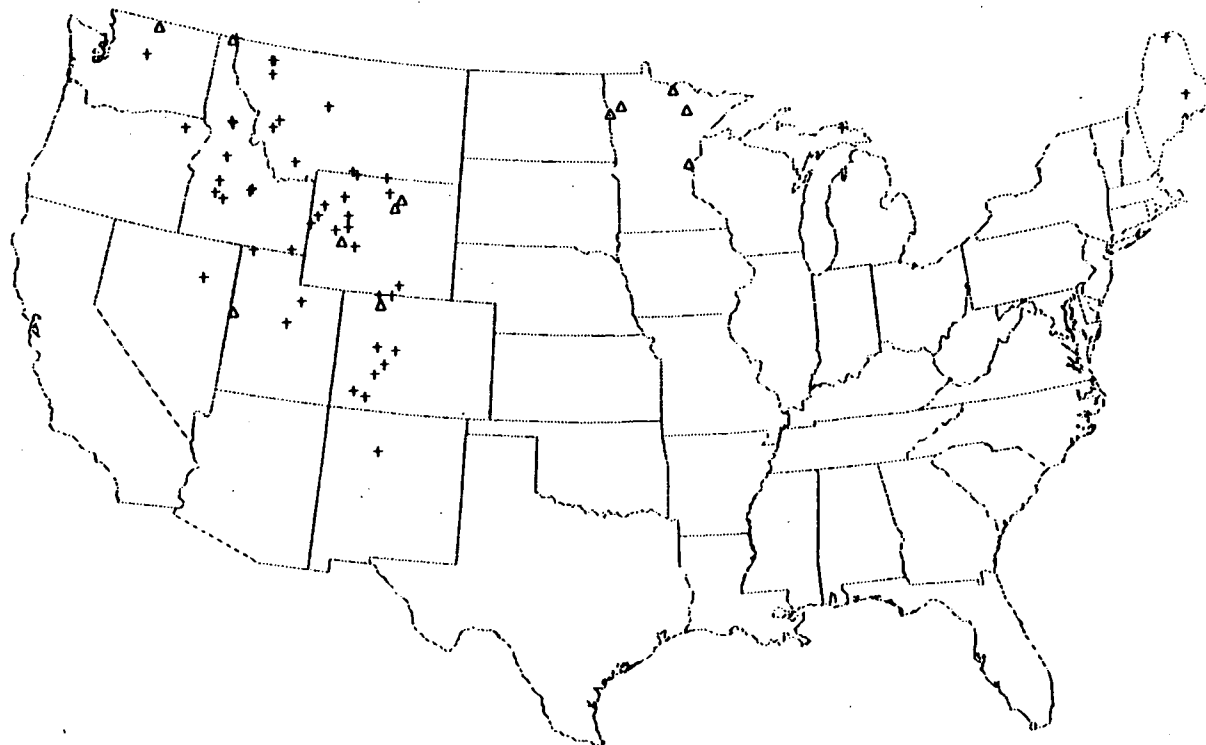
+ CLUS816 : CLUSNAME = 'SN1' -> 48 of 816
△ CLUS816 : CLUSNAME = 'SN2' -> 12 of 816

0   Miles   1000

STATES / CLUS816 / 'PF'

+ CLUS816 : CLUSNAME = 'PF' -> 54 of 816

0   Miles   1000

STATES / CLUS816 / ,'IR','IF','HI'
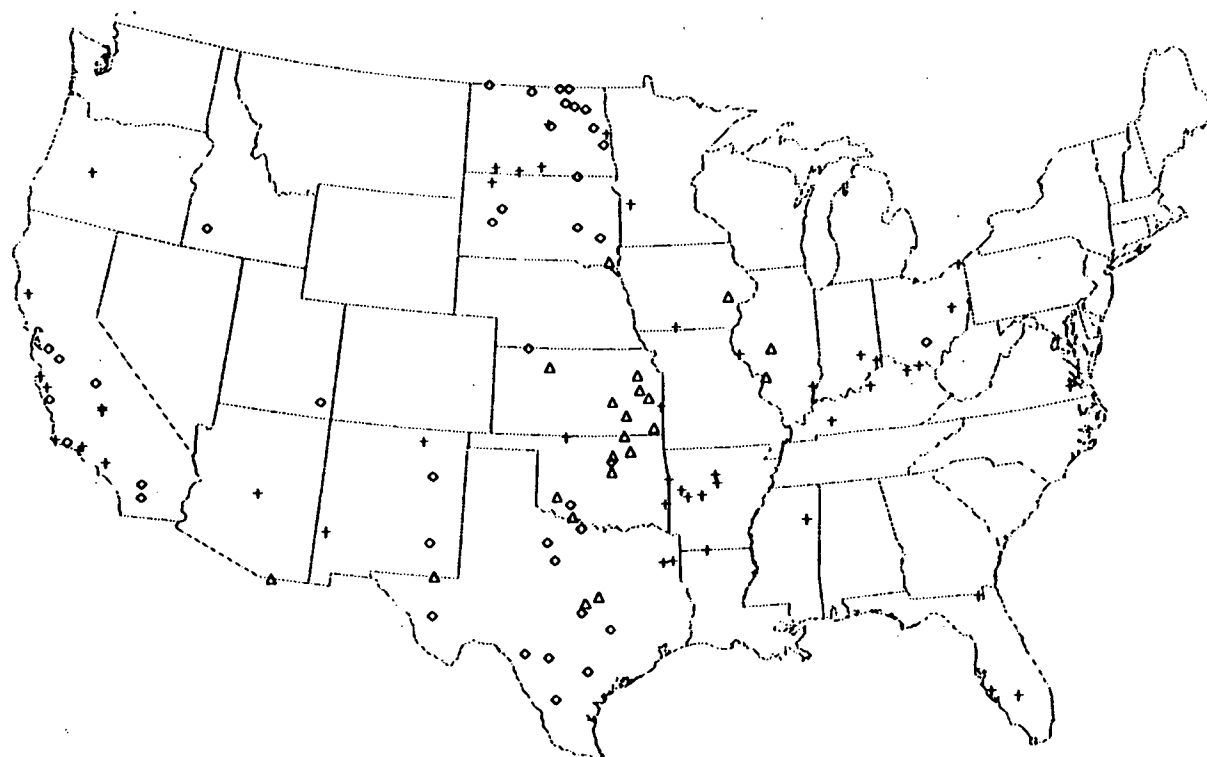
+ CLUS816 : CLUSNAME = 'IR' -> 49 of 816
△ CLUS816 : CLUSNAME = 'IF' -> 21 of 816
○ CLUS816 : CLUSNAME = 'HI' -> 40 of 816

0   Miles   1000

Monthly Predictability

Daily Predictability

Seasonal Predictability

Weekly Predictability
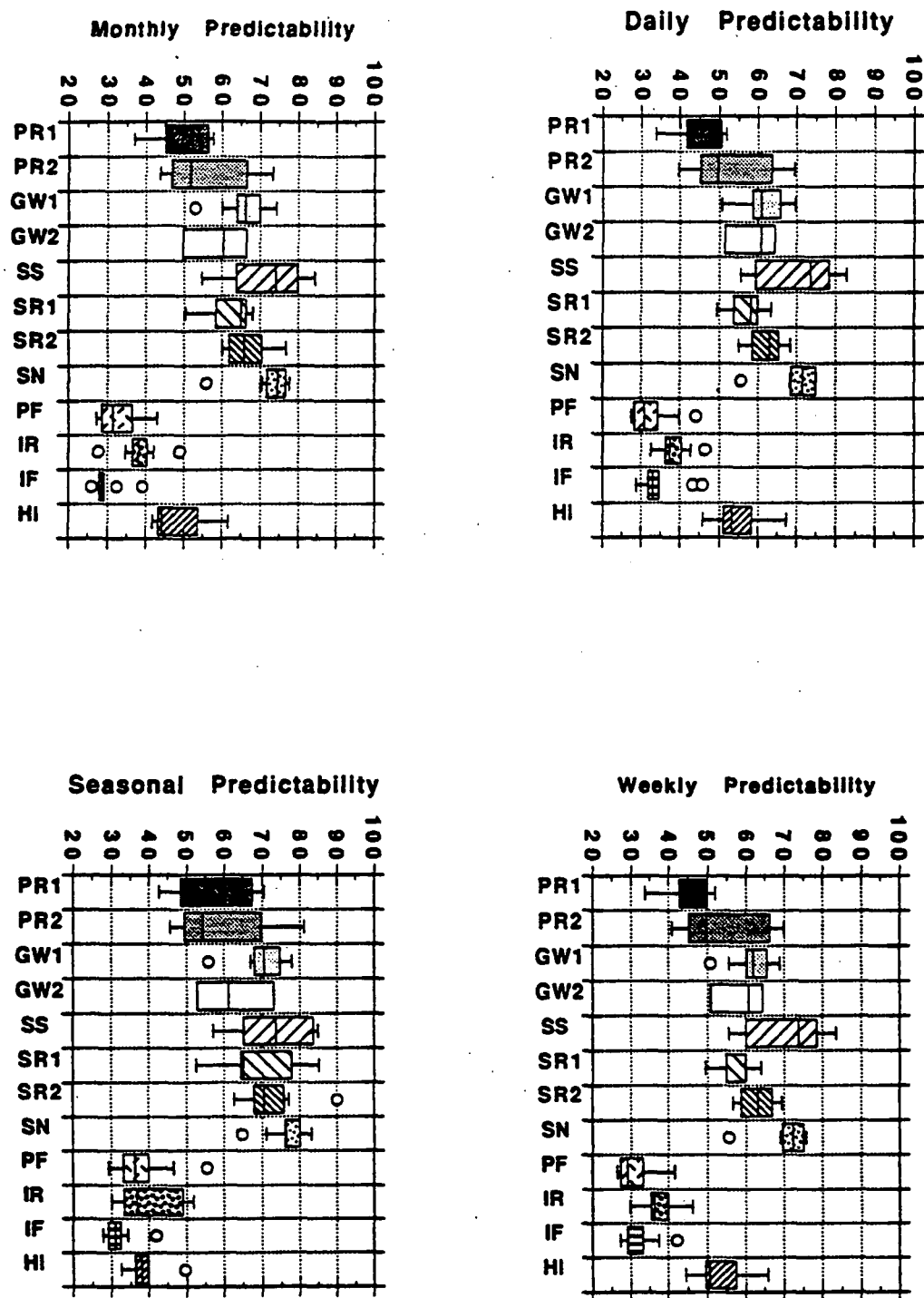
Figure 25. Range of values for Colwell's index of predictability calculated for 118 sites in 12 clusters for each of four different time steps (daily, weekly, monthly, seasonally) over a common 36-yr period. Each box encloses 50% of observed values (median = horizontal line). Observed range is contained within upper and lower bars except for extreme outliers (circles). Stream type abbreviations are provided in Table 8.
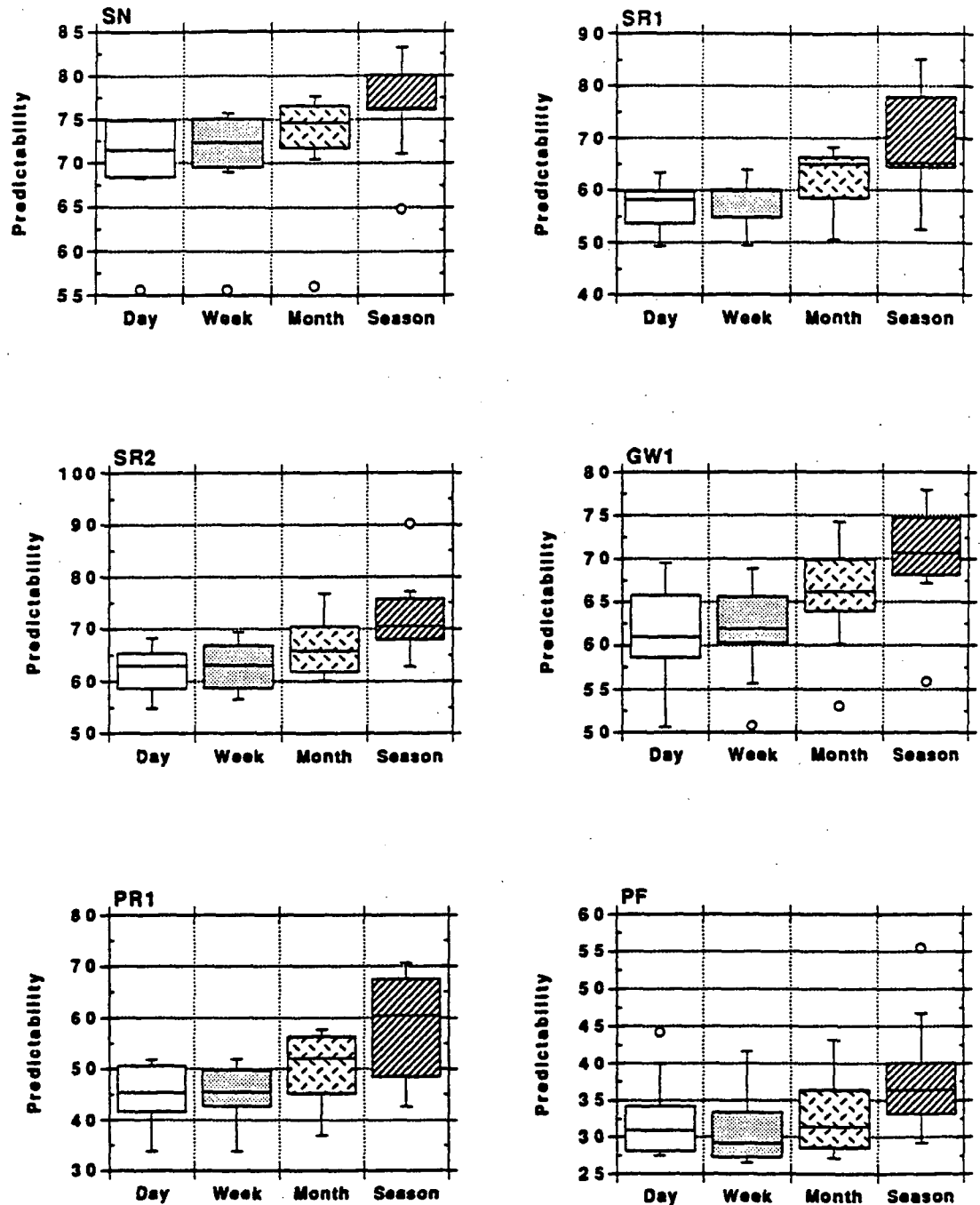
Figure 26. Range of values for Colwell's index of predictability calculated for four different time steps (daily, weekly, monthly, seasonally) for six stream groups. Interpretation as in Figure 25. Stream type abbreviations are given in Table 8.
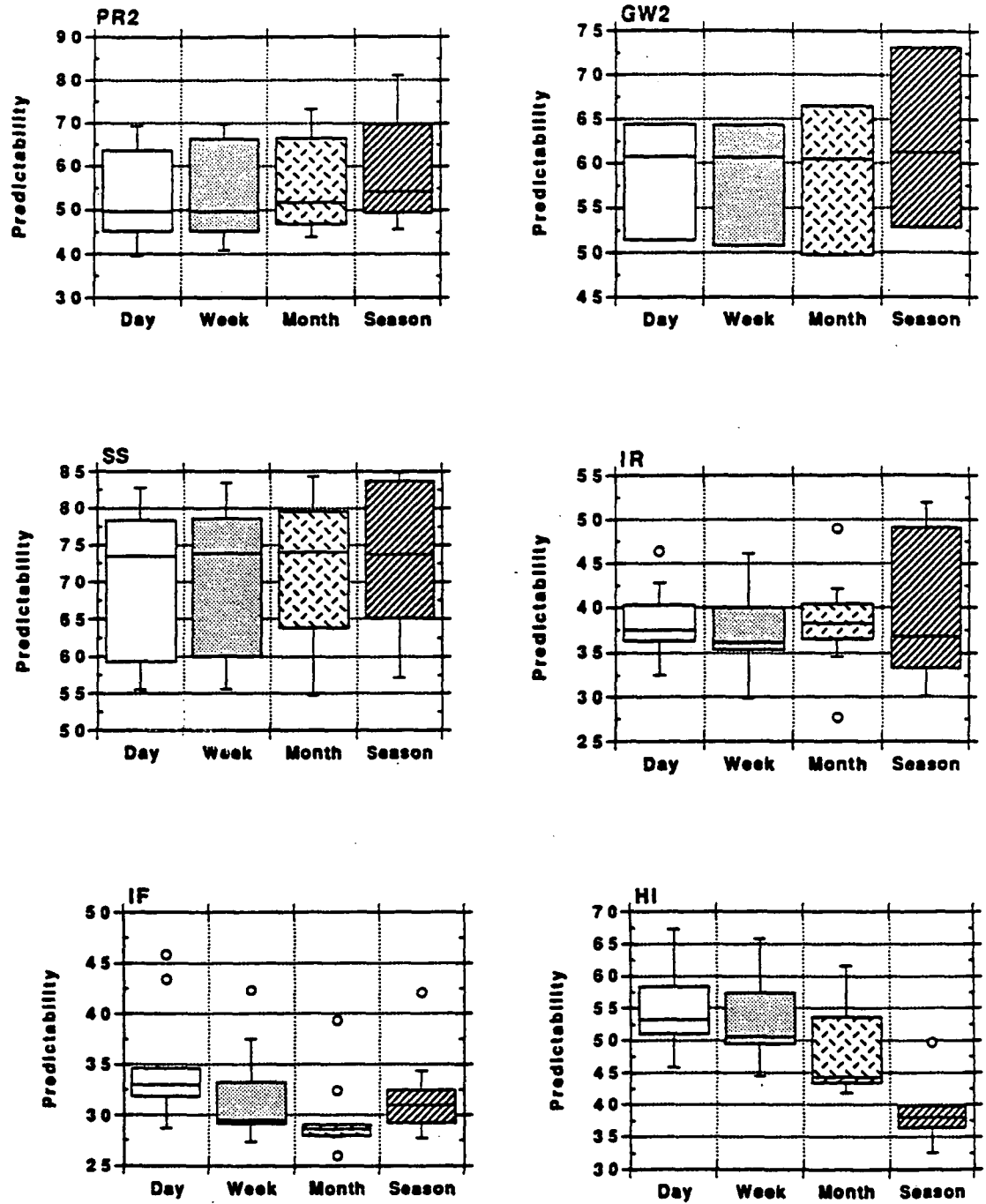
Figure 27. Range of values for Colwell's index of predictability calculated for four different time steps (daily, weekly, monthly, seasonally) for six stream groups. Interpretation as in Figure 25. Stream type abbreviations are given in Table 8.
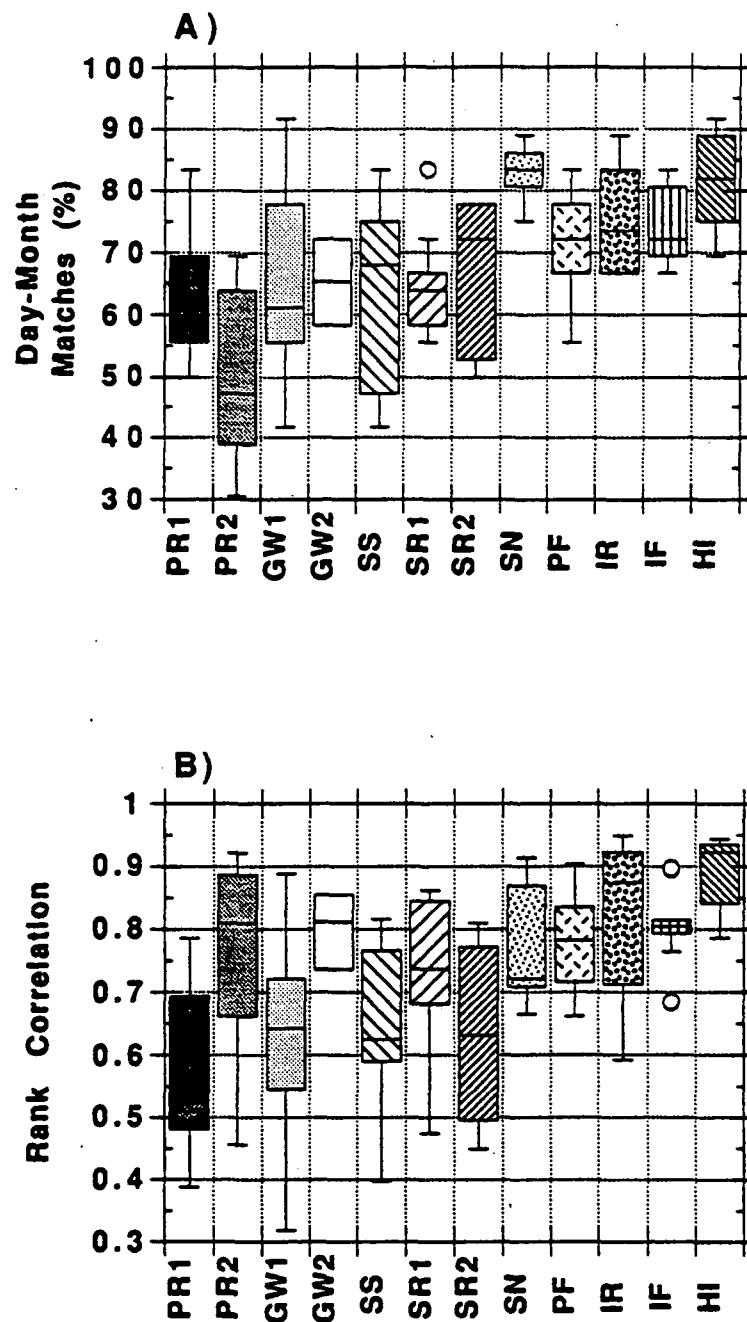
Figure 28. Range of values for 12 stream types over a common 36-yr record for
A) proportion of matches for maximum daily flow and maximum
monthly average, and B) rank correlation coefficient between
maximum daily flows and annual maximum flows. Interpretation as
in Figure 25.
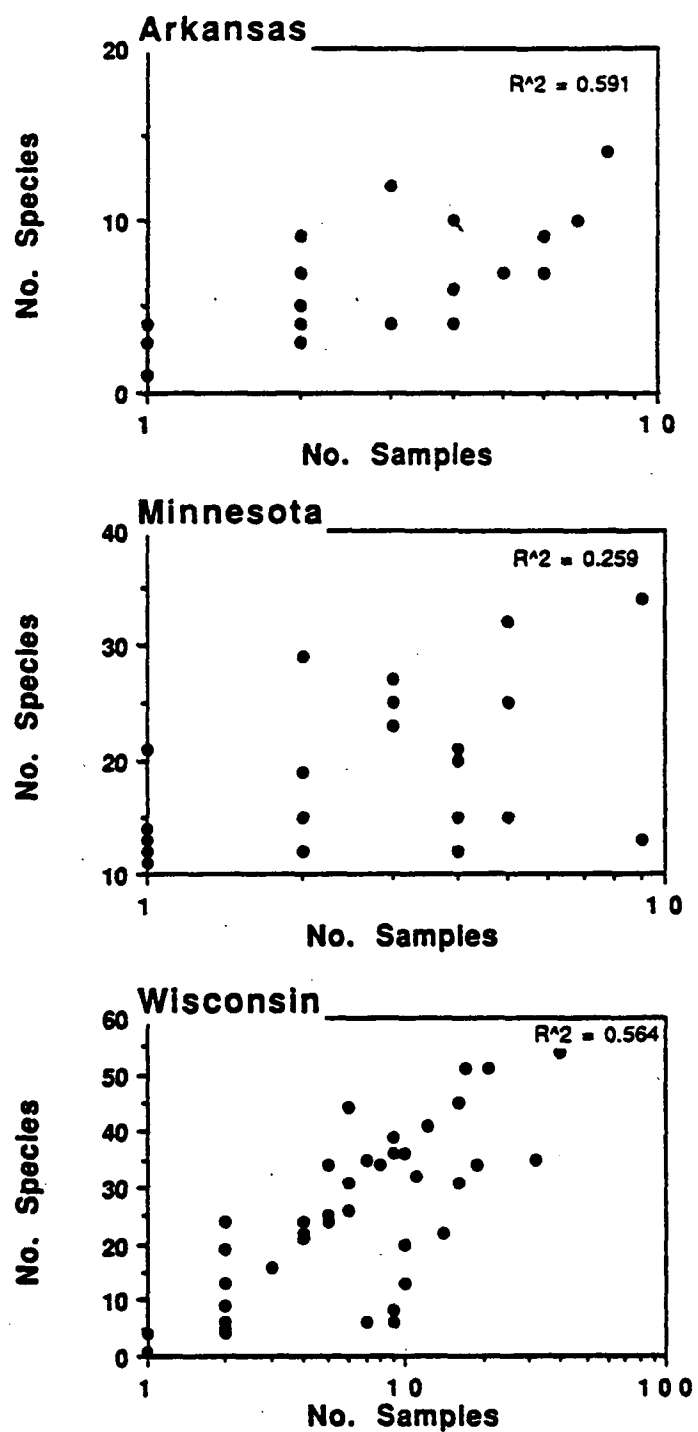
Figure 29. Association between number of samples and $\log_{10}$ of number of species for AR, MN, WI sites.
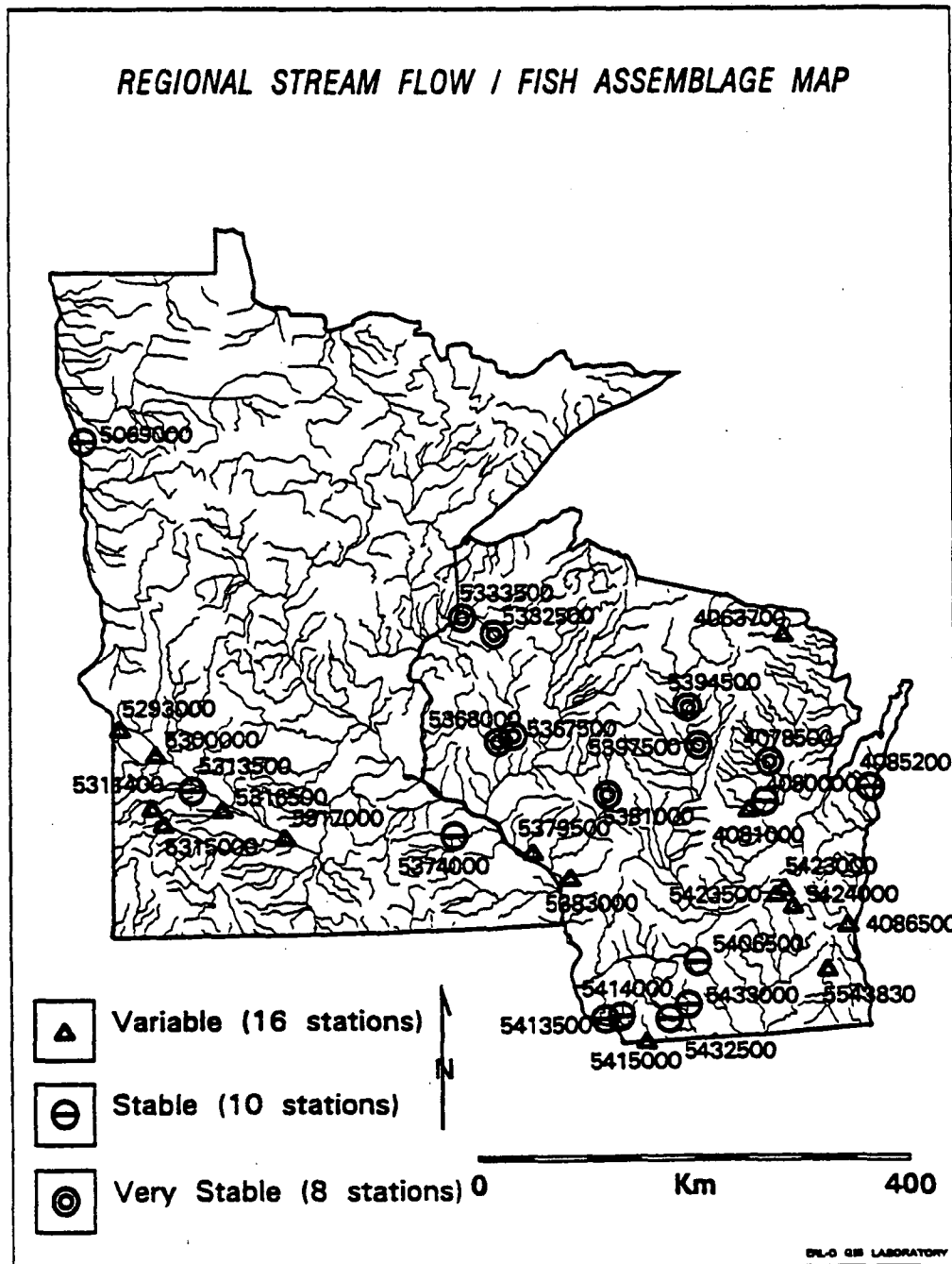
Figure 30. Geographical location of 34 WIMN sites, coded by stream gauge number. Symbols describe similar sites based on functional description of fish communities (see text for details).

150

WIMN (34 Sites)

R^2 = 0.385
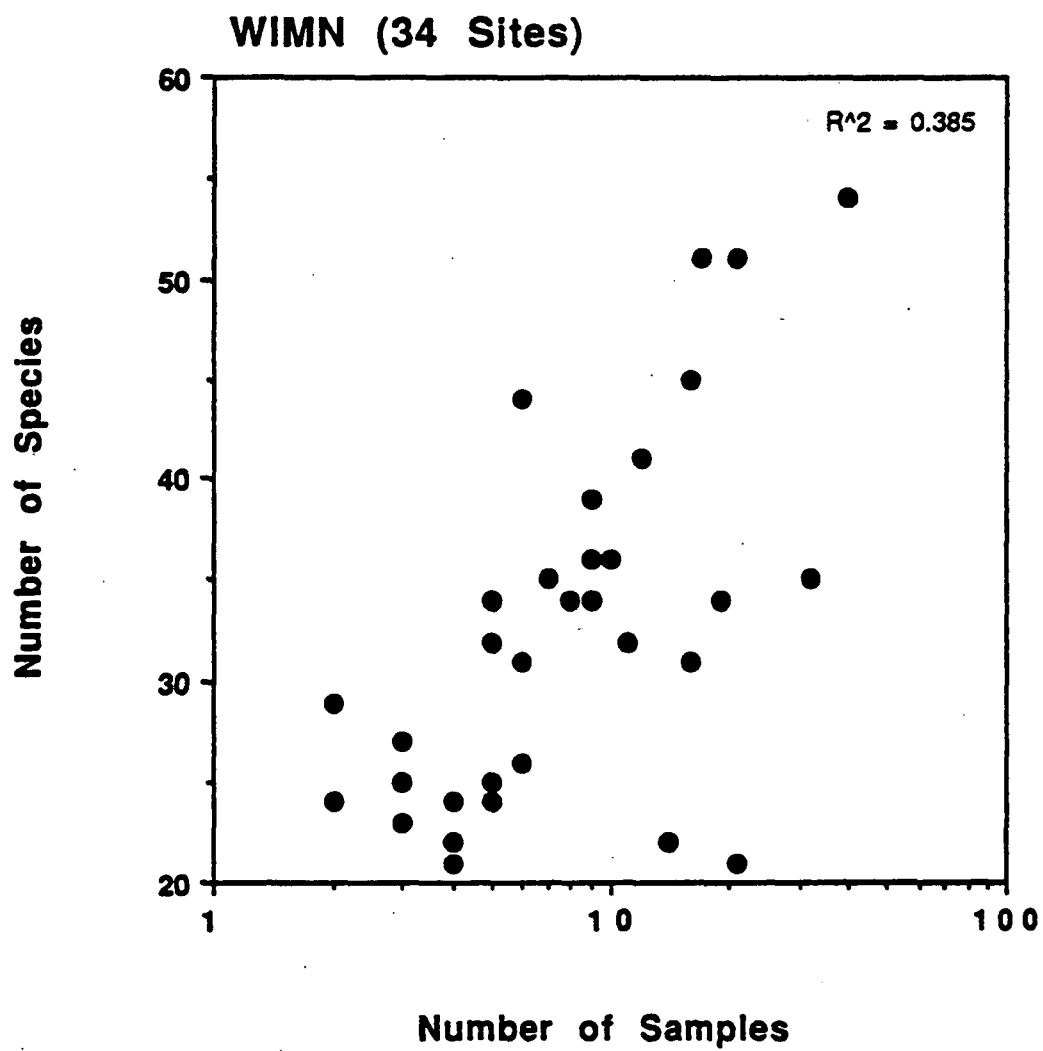
Figure 31. Relationship between number of samples and number of species
collected for 34 WIMN sites.
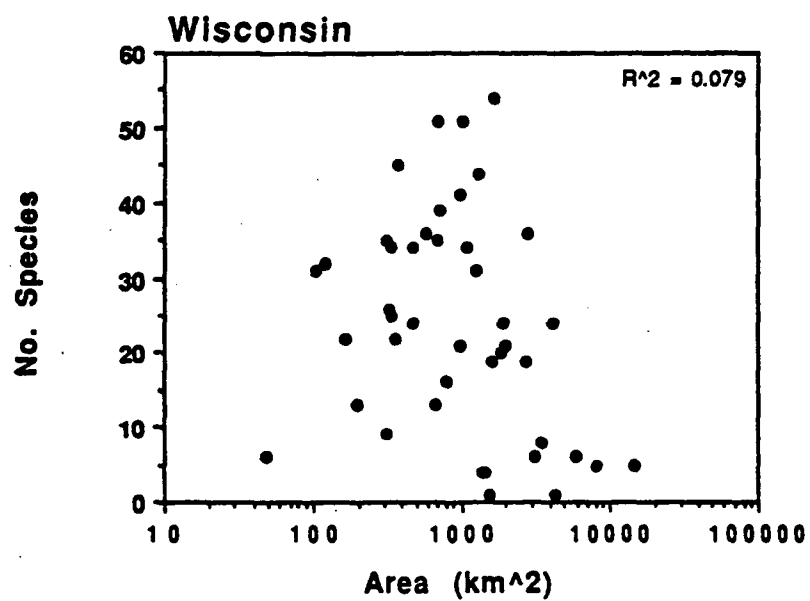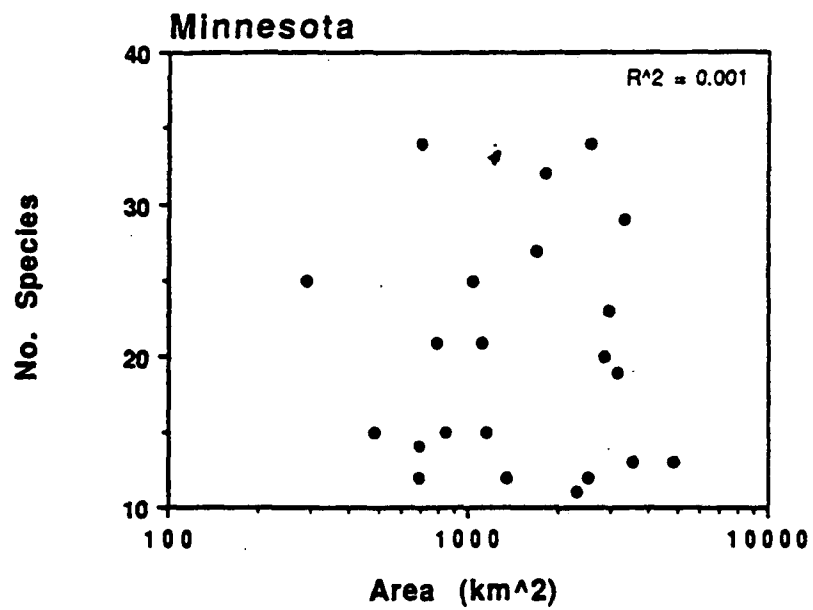
Figure 32. Relationship between number of species and catchment area for all 22 MN and 44 WI candidate sites.

WIMN

R^2 = 0.004

No. Species

Area (km^2)
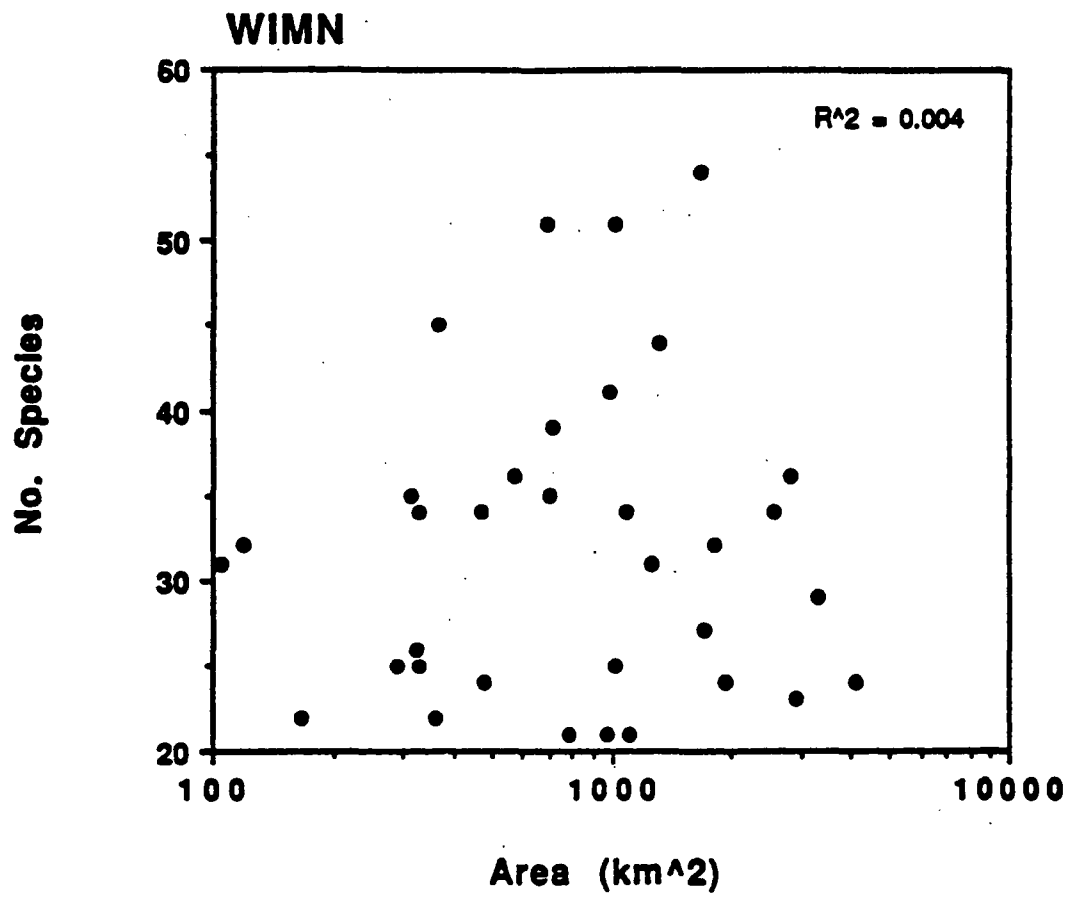
Figure 33. Relationship between number of species and catchment area for 34 WIMN sites.

LSR

SOS
BMS
SRL
QBS

NHS

SRL

BNT

4 clusters
(2 levels of division)

① ② ③ ④

WAE
SPS

PMK

NOP

BLC

8 clusters
(3 levels of division)

4063700	4086500						
4085200	5423000	4078500	5332500	5069000	5313500	5406500	5379500
5423500	5424000	4080000	5333500	5293000	5317000	5413500	5383000
	5543830	4081000	5367500	5300000	5374000	5415000	5414000
		5381000	5368000	5311400		5433000	
			5394500	5315000			
			5397500	5316500			
				5432500			
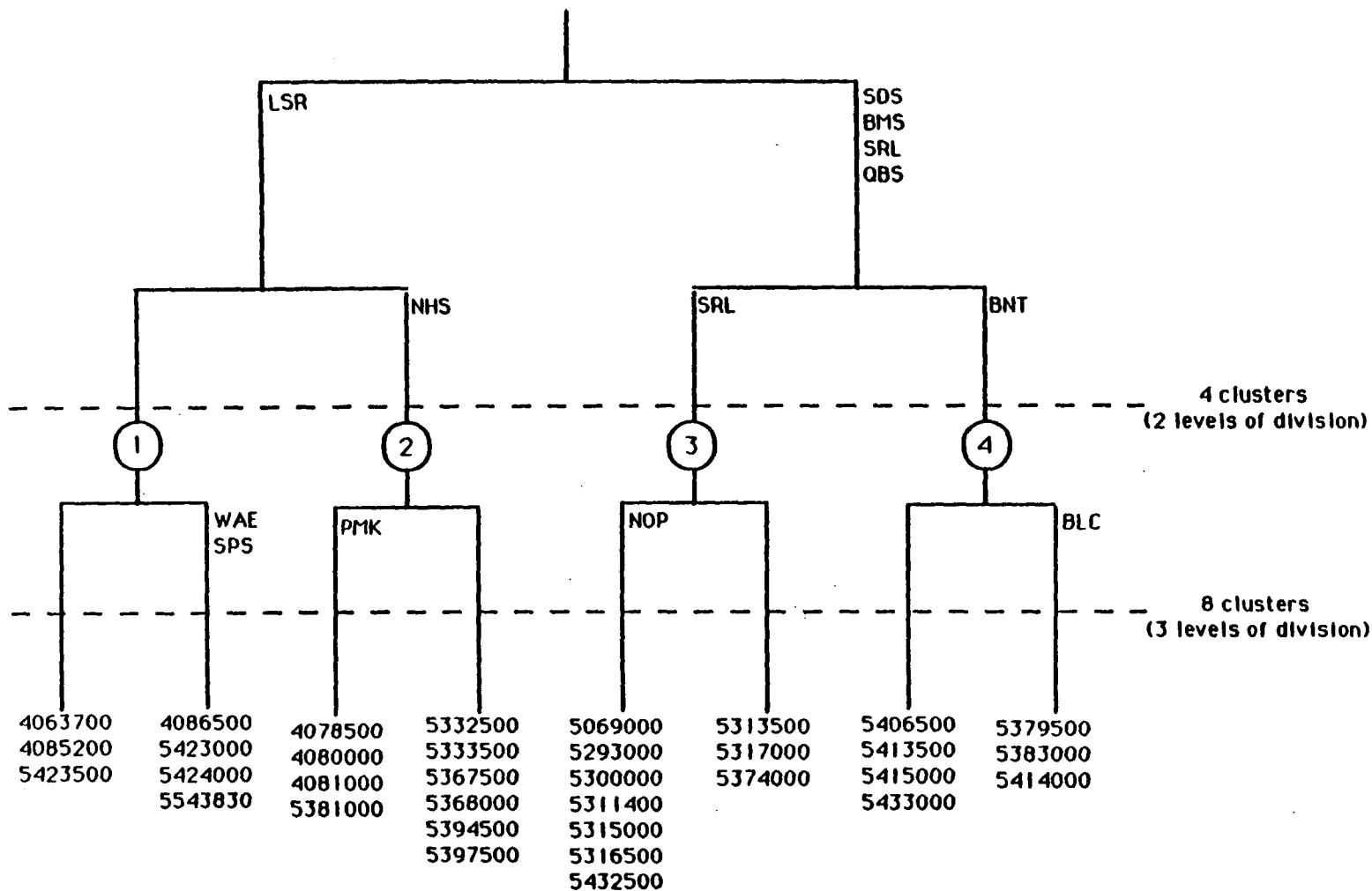
Figure 34. TWINSPAN dendrogram generated for 34 WIMN sites from the binary taxonomic data. "Indicator" species that discriminate among-group differences at each branch point are shown with 3-letter abbreviations (see Table 16 for species names). Two, 4, or 8 clusters can be identified for 1, 2, and 3 levels of division, respectively. Numbers in circles indicate four TWINSPAN groups for 2-level division.

REGIONAL STREAM FLOW / FISH ASSEMBLAGE MAP

◯	TWIN 1
⊖	TWIN 2
☐	TWIN 3
⊟	TWIN 4

0   Km   400
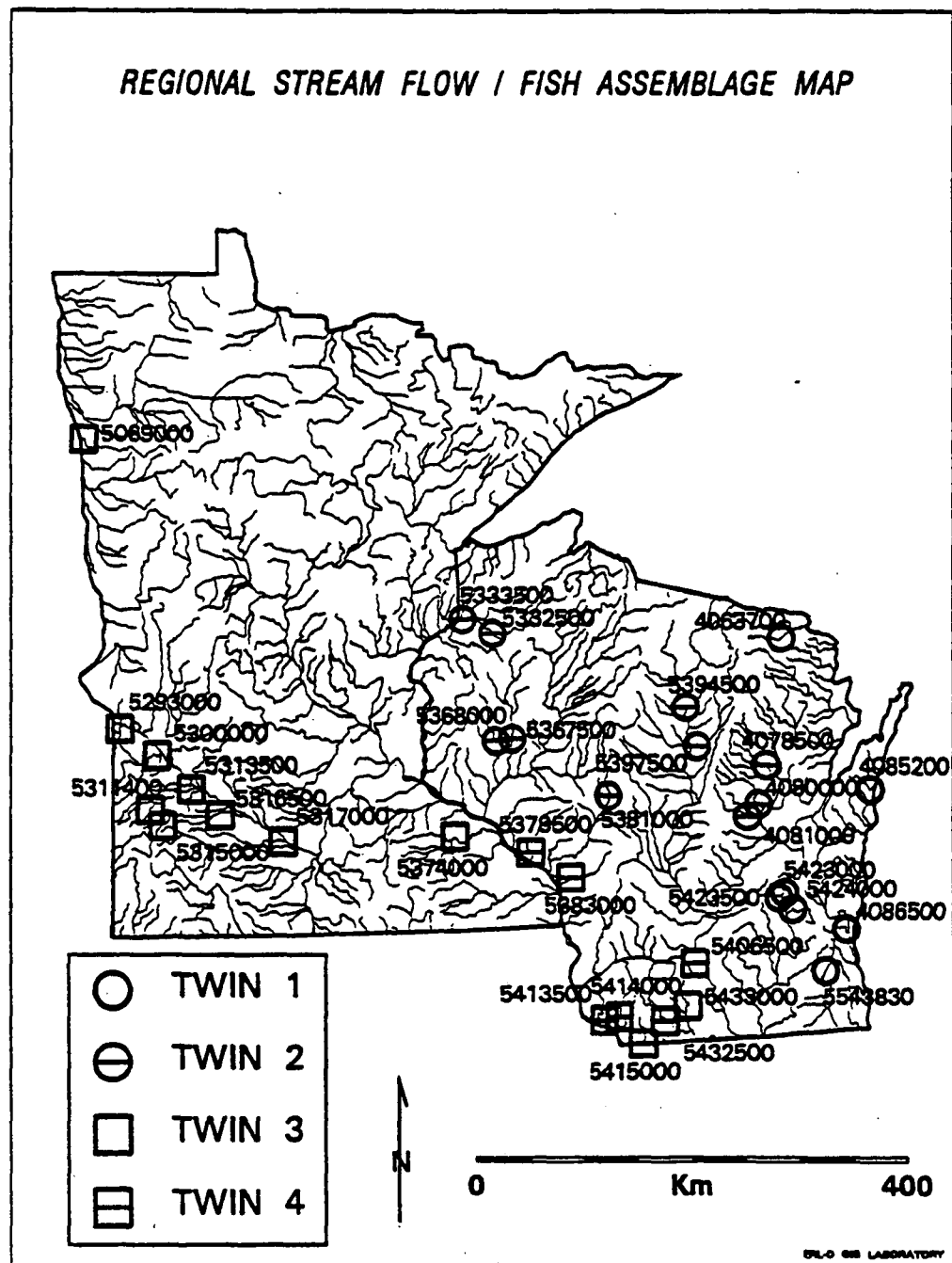
Figure 35. Geographical location of 34 WIMN sites grouped according to affiliation defined in four-group TWINSPAN classification.
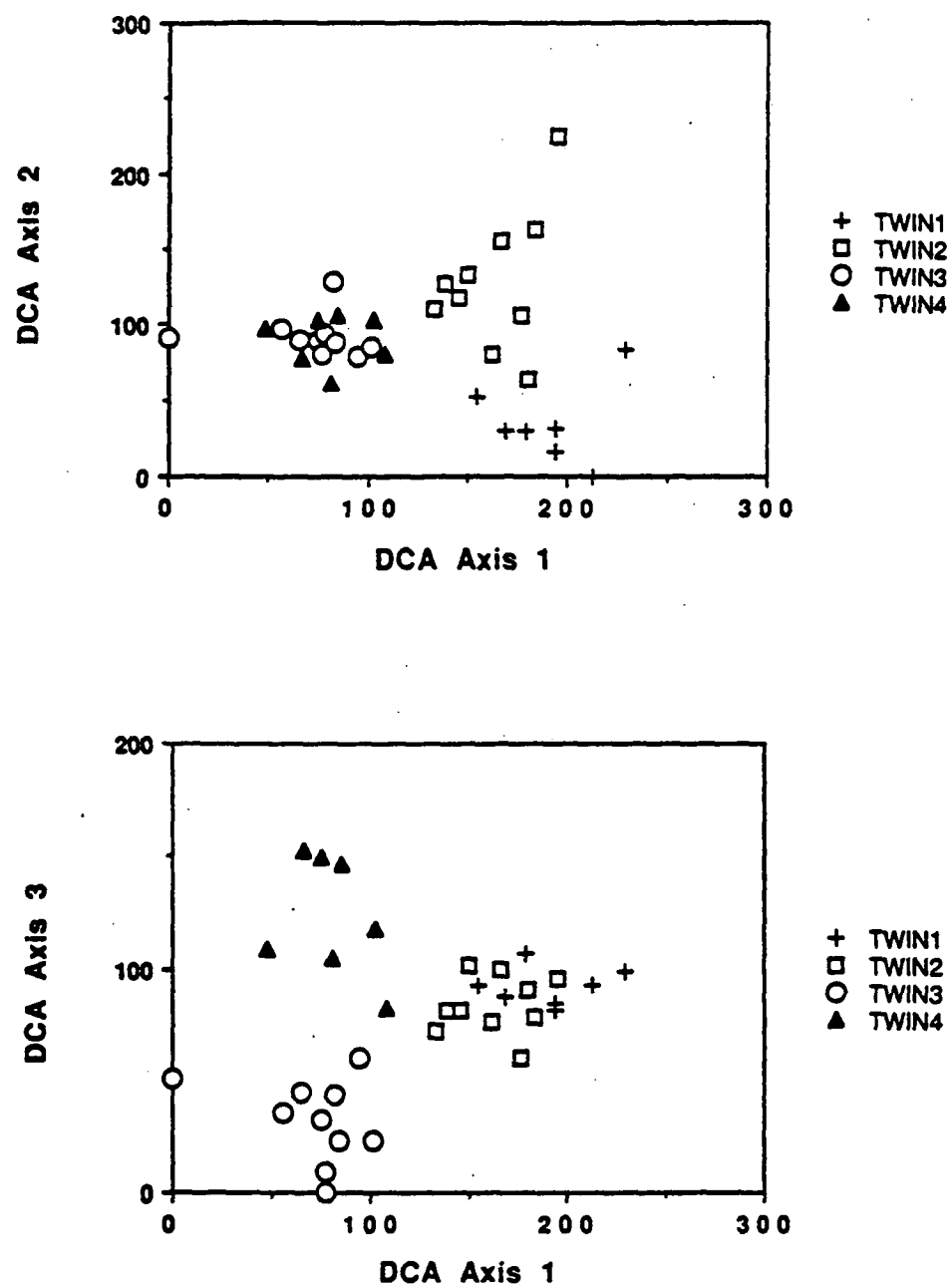
Figure 36. Positions of individual WIMN sites plotted according to scores on DCA axes generated from binary taxonomic data. Sites are coded by four TWINSPAN groups indicated in Figure 34.

Figure 37. Positions of 106 species plotted according to scores on first two DCA axes generated from binary taxonomic data. Species abbreviations not in parentheses are indicator species (see TWINSPAN dendogram, Fig. 34). Species abbreviations are explained in Table 16.

```
                 4 5 5 5 5 5 5 5 5 4 4 5 5 5 5 5 4 5 5 5 5 5 5 5 5 4 5 4 5 5 5 5 5 5 5
                 0 4 4 3 4 2 3 3 3 0 0 4 5 3 3 0 0 3 3 3 3 3 3 3 0 4 0 3 4 0 3 4 4 4
                 6 2 2 1 1 9 0 1 1 8 8 2 4 1 7 8 7 3 3 6 9 6 8 9 8 3 8 1 3 6 7 0 1 1
                 3 3 3 5 5 3 0 1 7 7 6 4 3 6 9 3 8 3 2 7 4 8 1 7 0 3 5 3 2 9 4 6 3 4
                 7 0 5 0 0 0 0 4 0 0 5 0 8 5 5 0 5 5 5 5 5 0 0 5 0 0 2 5 5 0 0 5 5 0
                 0 0 0 0 0 0 0 0 0 0 0 0 3 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
                 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
```

```
    0.45 +
         |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
         |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
         |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
         |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
    0.4  +XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
         |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
         |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
         |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
         |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
    0.35 +XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
         |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
  s      |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
  e      |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
  m      |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
  i  0.3 +XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
  -      |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
  p      |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
  a      |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
  r      |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
  t 0.25 +XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
  i      |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
  a      |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
  l      |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
         |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
  R  0.2 +XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
  -      |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
  s      |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
  q      |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
  u      |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
  a 0.15 +XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
  r      |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
  e      |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
  d      |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXX
         |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXX
    0.1  +XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXX
         |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXX
         |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXX
         |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXX
         |XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXXXX
    0.05 +XXXXXXXXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXX   XXXXXXXXXXXX
         |XXXXXXXXXXXXX   XXXXXXXXX   XXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXX   XXXXXXXXXXXX
         |XXXXXXXXXXXXX   XXXXXXXXX   XXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXX   XXXXXXXXXXXX
         |XXXXXXX  XXXX  XXXXXXXXX   XXXXXXXXXXXXXXXXXX   XXXXXXXXXXXXXXXXXXXXXX   XXXXXXXXXXXX   XXXXXXXXXXXX
         |XXXXXXX   .   .  XXXXXXXXX   XXXXXXXXX   XXXXXXX   XXXXXXXXXXXXX   XXXXXXX   XXXX  XXXXXXX   XXXX   XXXXXXX
    0    +.  XXXX   .   .   XXXX   .   .   .   XXXXXXX   .   .   .   XXXX  XXXXXXX  XXXX   .   XXXX   .   .   .   .   .   XXXX   .
```
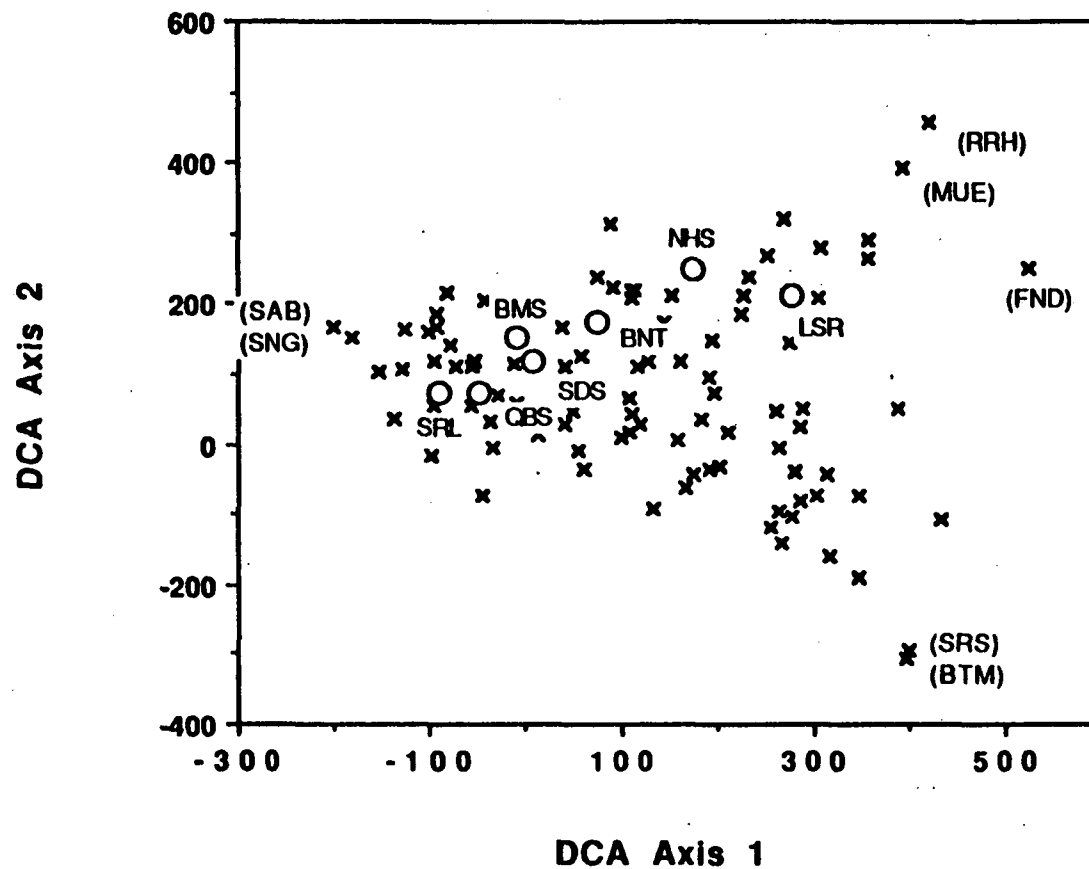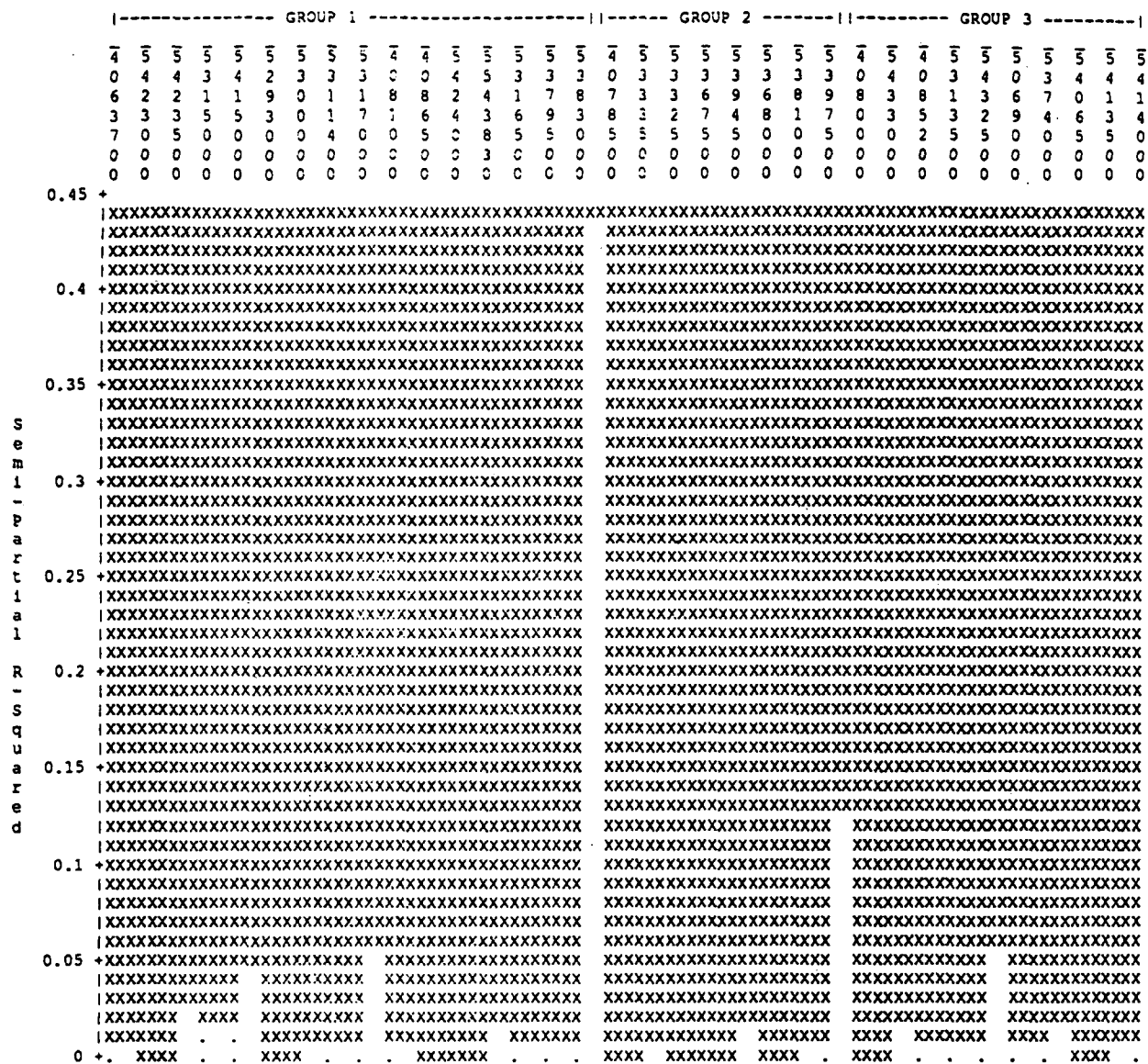
Figure 38. Hierarchical dendrogram generated by Ward's method using
the 36 site x 25 functional attribute matrix. Group 1 is
well-separated from Groups 2 + 3 (semi-partial r-squared
distance measure = ca. 0.45), while Group 2 separates from
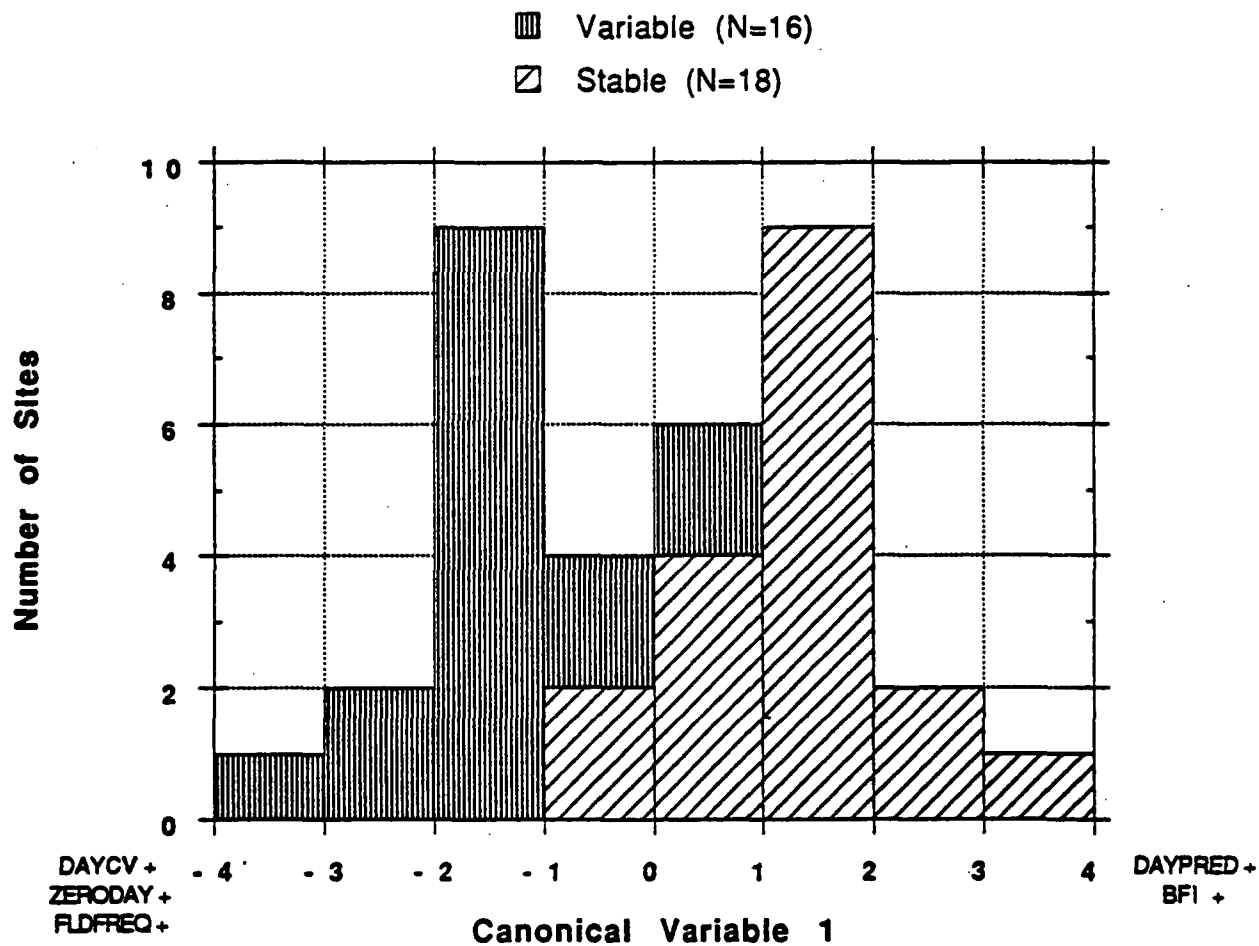Group 3 at a much shorter distance measure of ca. 0.12.

Figure 39. Location of 34 individual WIMN sites with respect to scores on the
first canonical variable. Sites are coded according to membership in
either of two groups, Variable or Stable sites. Hydrologic variables
that have significant correlations with the canonical variable are
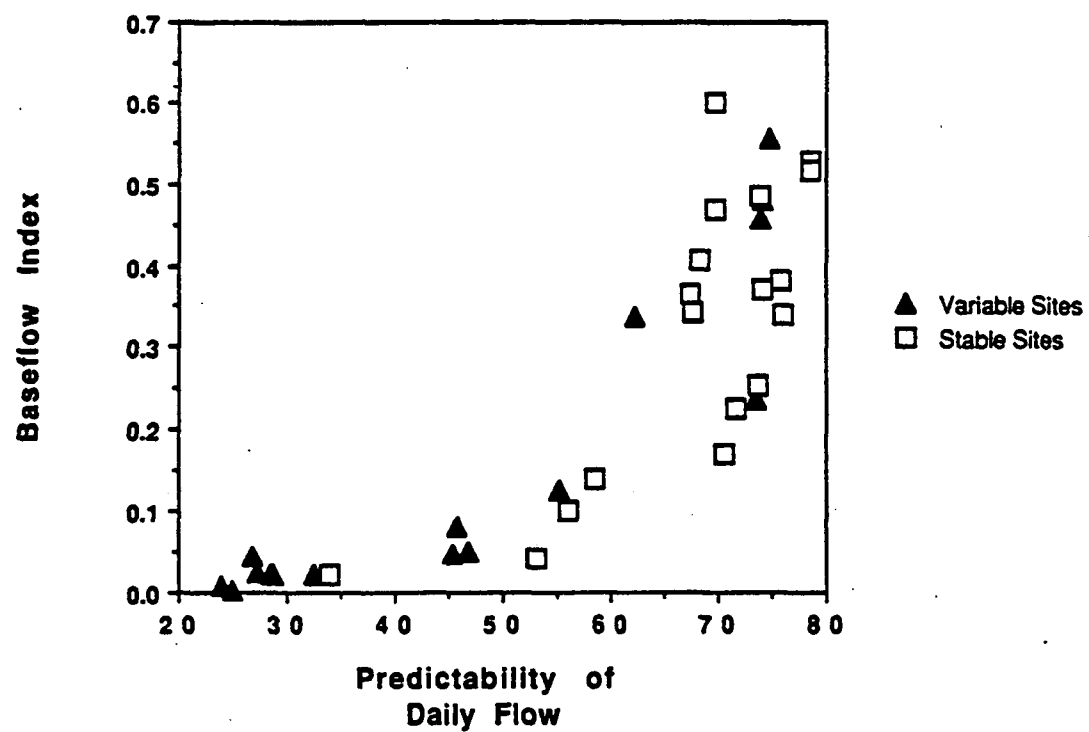indicated at either end of the horizontal axis.

Figure 40. Locations of 34 individual WIMN sites in bivariate space defined by
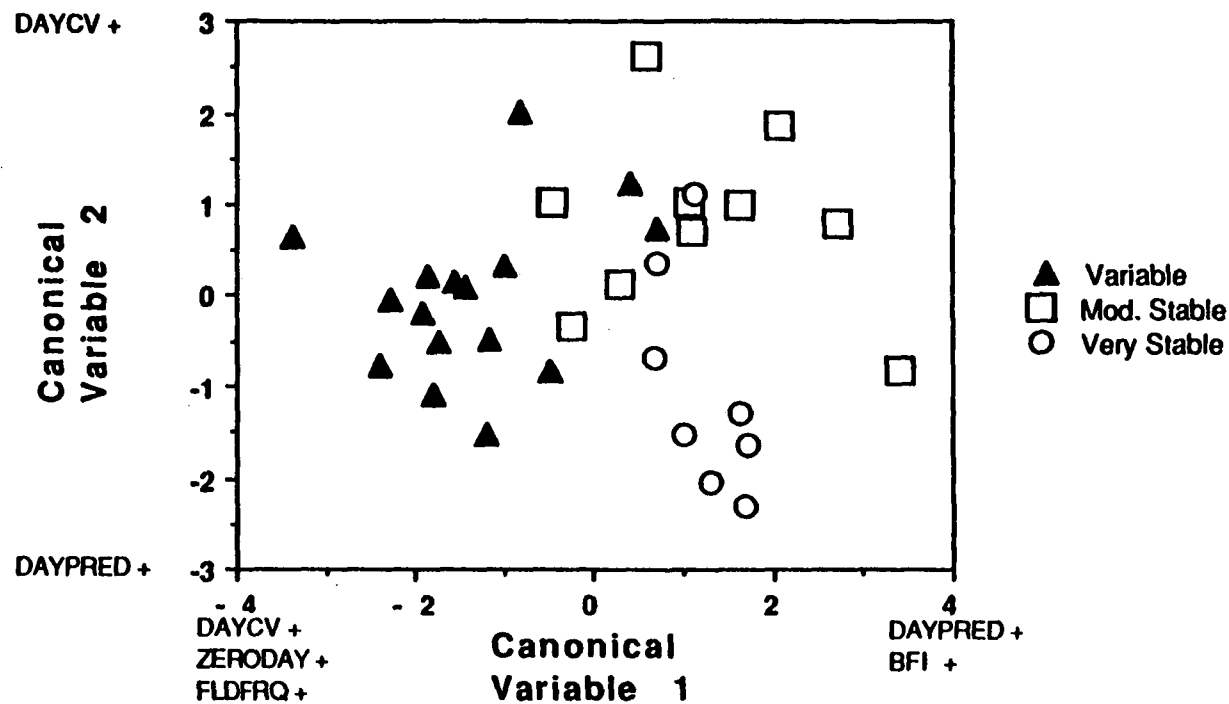the hydrologic variables DAYPRED and BFI. Sites are coded by
affiliation in one of two groups.

Figure 41. Locations of 34 individual WIMN sites based on their scores on the first two canonical variables in the 3-cluster case. Original hydrologic variables that are correlated with the canonical variables (see Table 20) are indicated by their abbreviations.
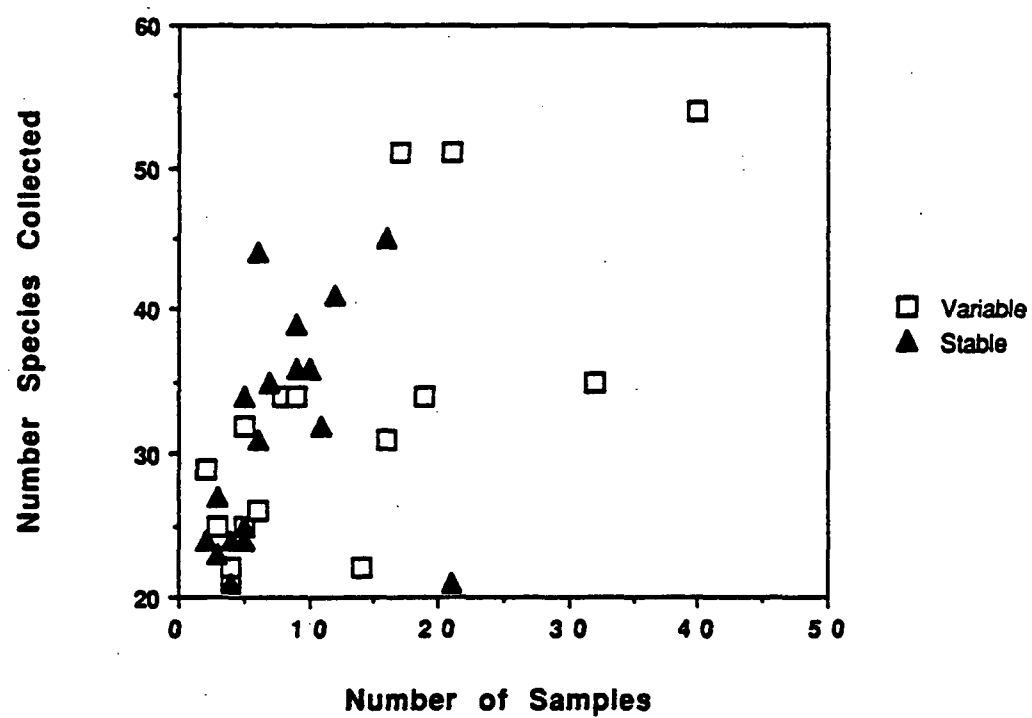
Figure 42. Relationship between number of species and number of samples collected for all 34 WIMN sites, coded by cluster affiliation (2-cluster case). For Variable sites, $r^2 = 0.43$, and for Stable sites, $r^2 = 0.29$.
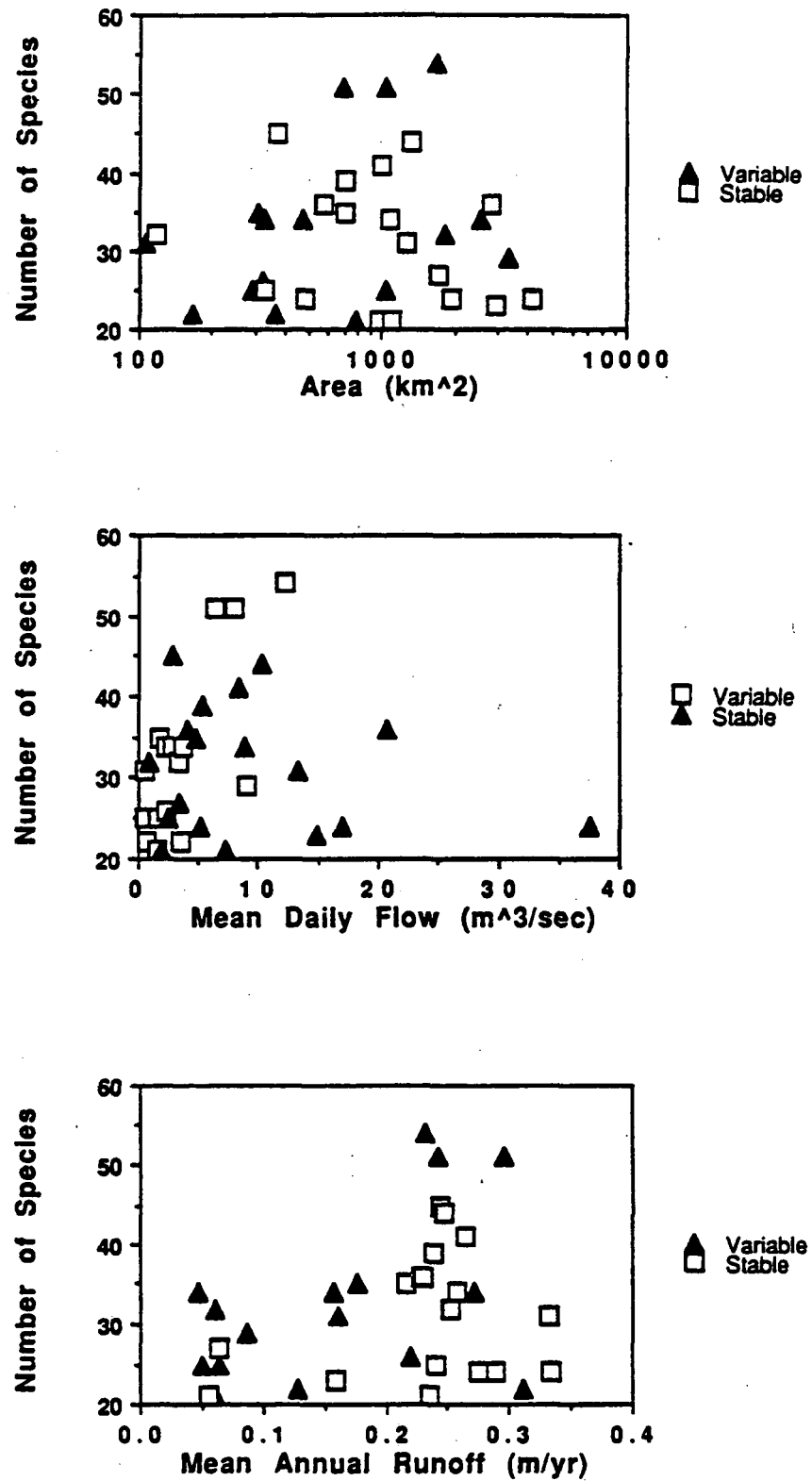
Figure 43. Relationship between number of species and three measures of catchment area collected for all 34 WIMN sites, coded by cluster affiliation (2-cluster case).
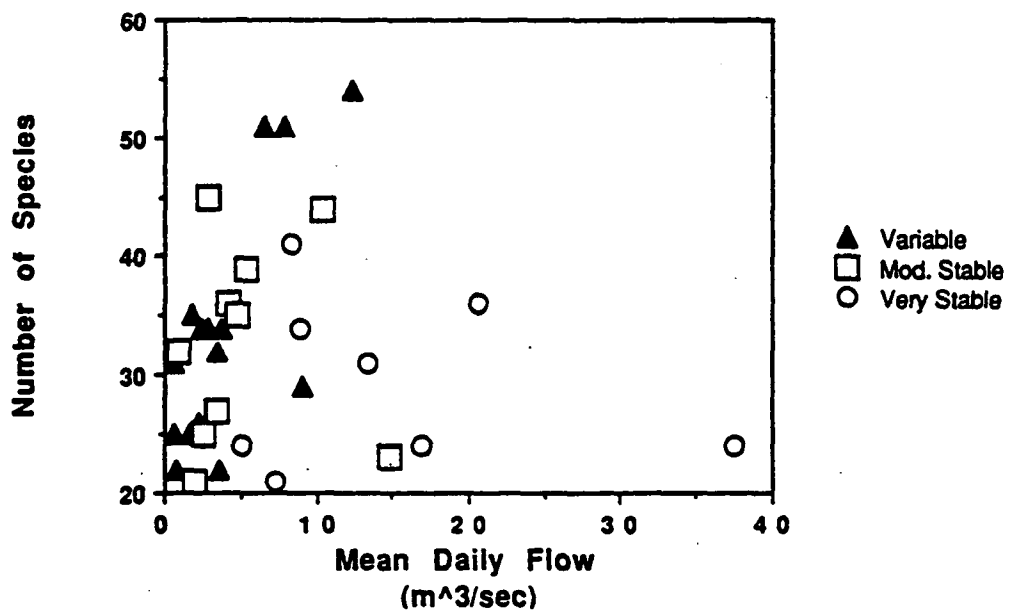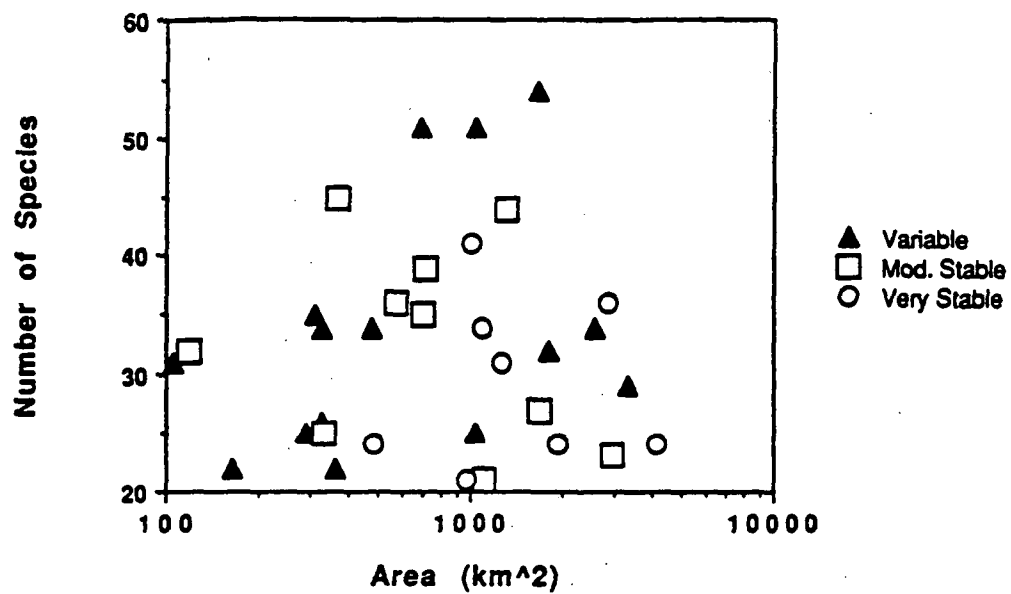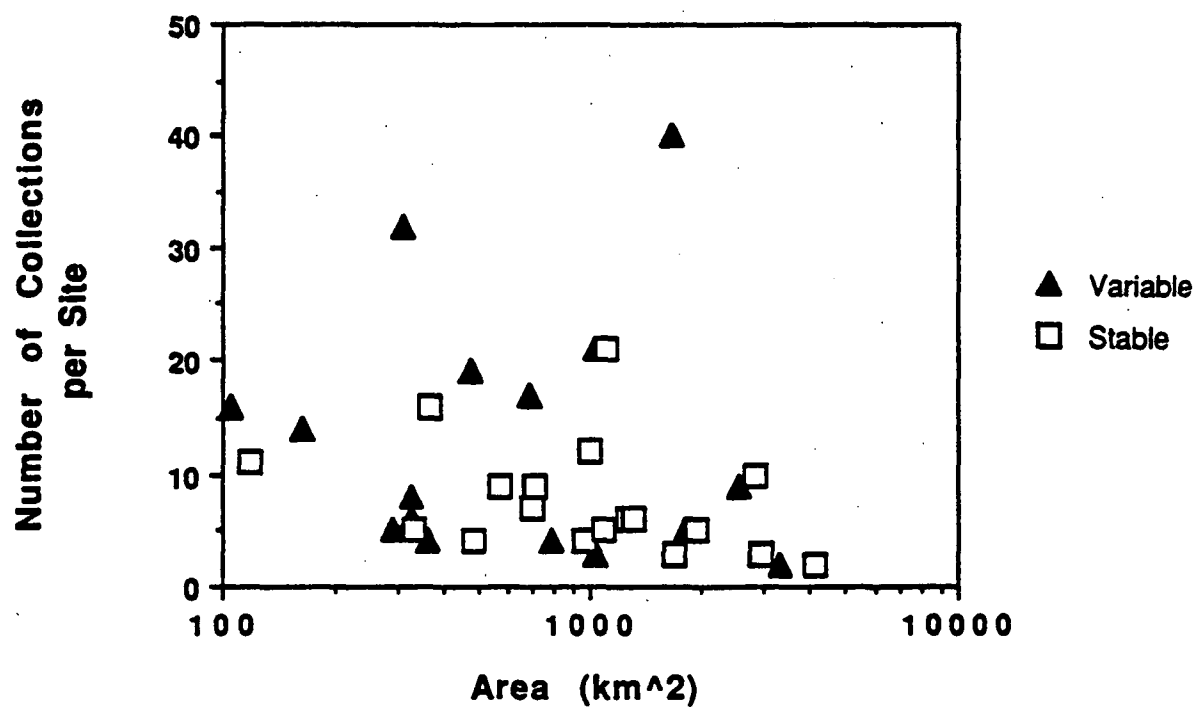
Figure 44. Relationship between number of species and two measures of
catchment area collected for all 34 WIMN sites, coded by cluster
affiliation (3-cluster case).

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Figure 45. Relationship between sampling intensity and catchment area for 34 WIMN sites, coded by cluster affiliation (2-cluster case).
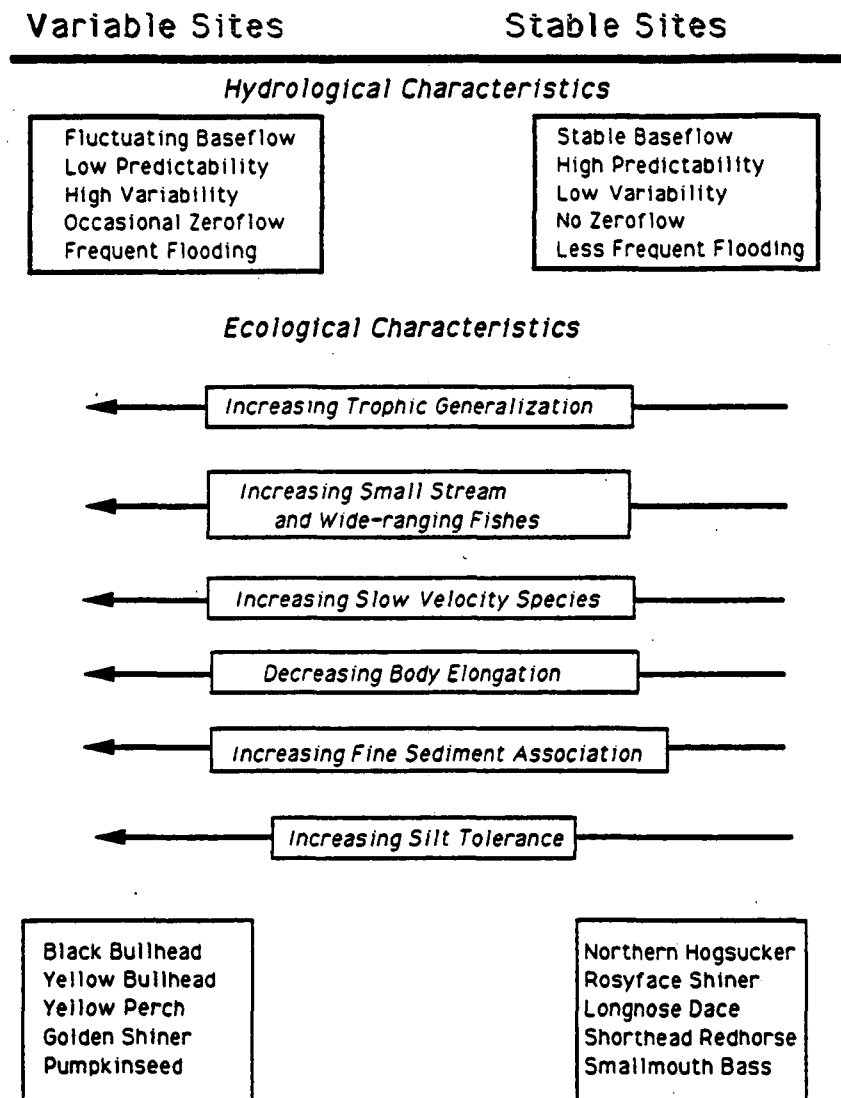
Variable Sites
Stable Sites

Hydrological Characteristics

Fluctuating Baseflow	Stable Baseflow
Low Predictability	High Predictability
High Variability	Low Variability
Occasional Zeroflow	No Zeroflow
Frequent Flooding	Less Frequent Flooding

Ecological Characteristics

← *Increasing Trophic Generalization* →

← *Increasing Small Stream and Wide-ranging Fishes* →

← *Increasing Slow Velocity Species* →

← *Decreasing Body Elongation* →

← *Increasing Fine Sediment Association* →

← *Increasing Silt Tolerance* →

Black Bullhead	Northern Hogsucker
Yellow Bullhead	Rosyface Shiner
Yellow Perch	Longnose Dace
Golden Shiner	Shorthead Redhorse
Pumpkinseed	Smallmouth Bass

Figure 46. Conceptual summary graph of relationships between hydrological and ecological characteristics for the 34 WIMN sites. Species that occur almost exclusively at one end of the hydrological-ecological gradient are indicated at the bottom of the figure.
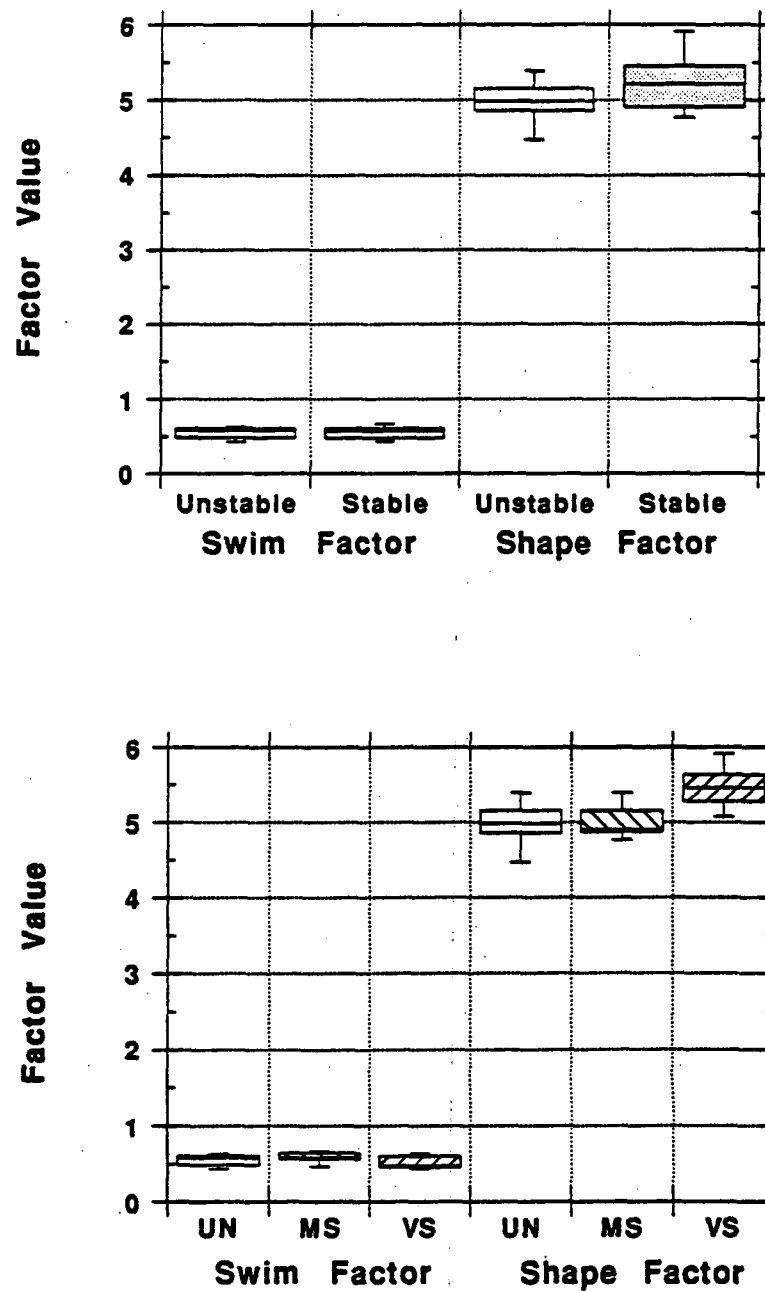
Figure 47. Mean group scores (+ 2se) for two body morphology attributes for the 2-cluster case (upper panel) and 3-cluster case (lower panel). For each cluster, box encloses 50% of observed values, with median value indicated by horizontal line within box. Upper and lower bars enclose upper and lower 25% of observations, respectively.
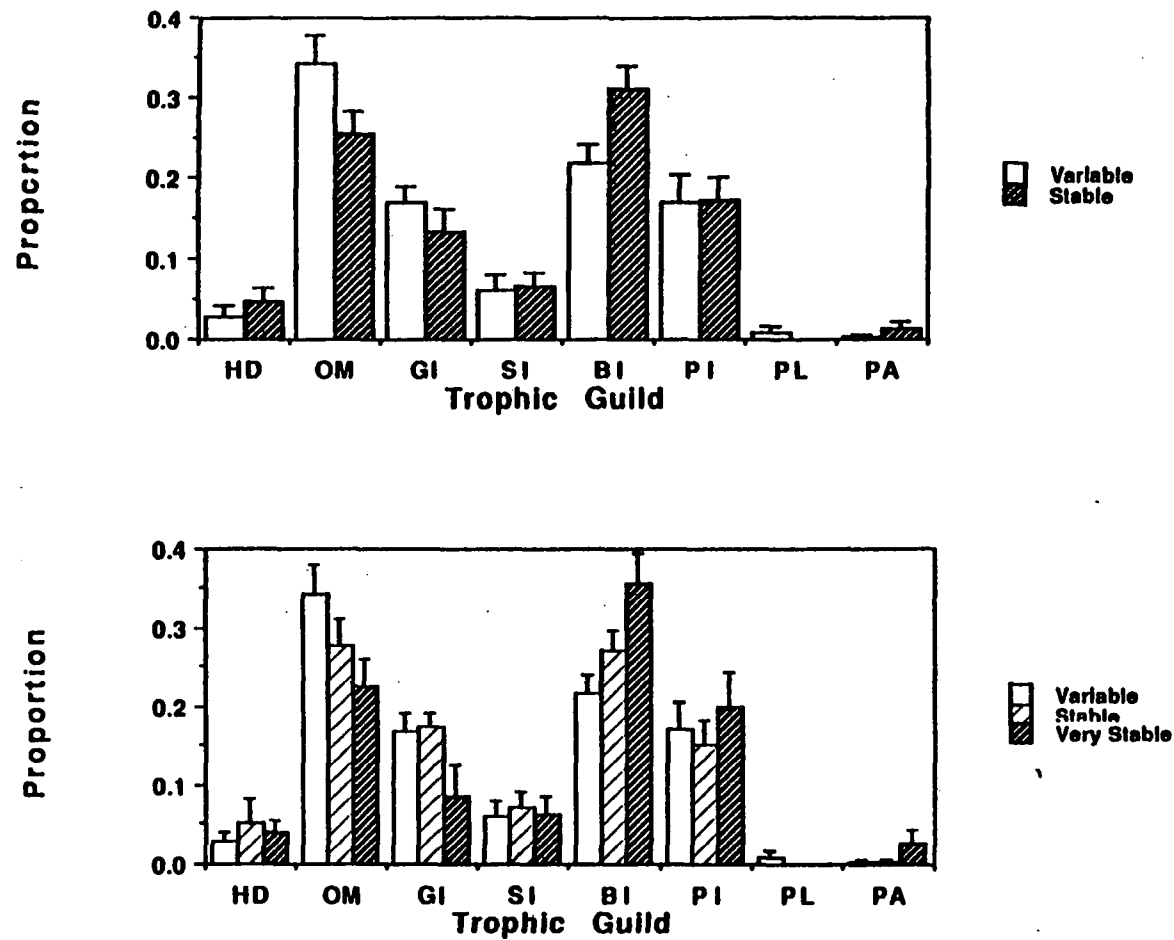
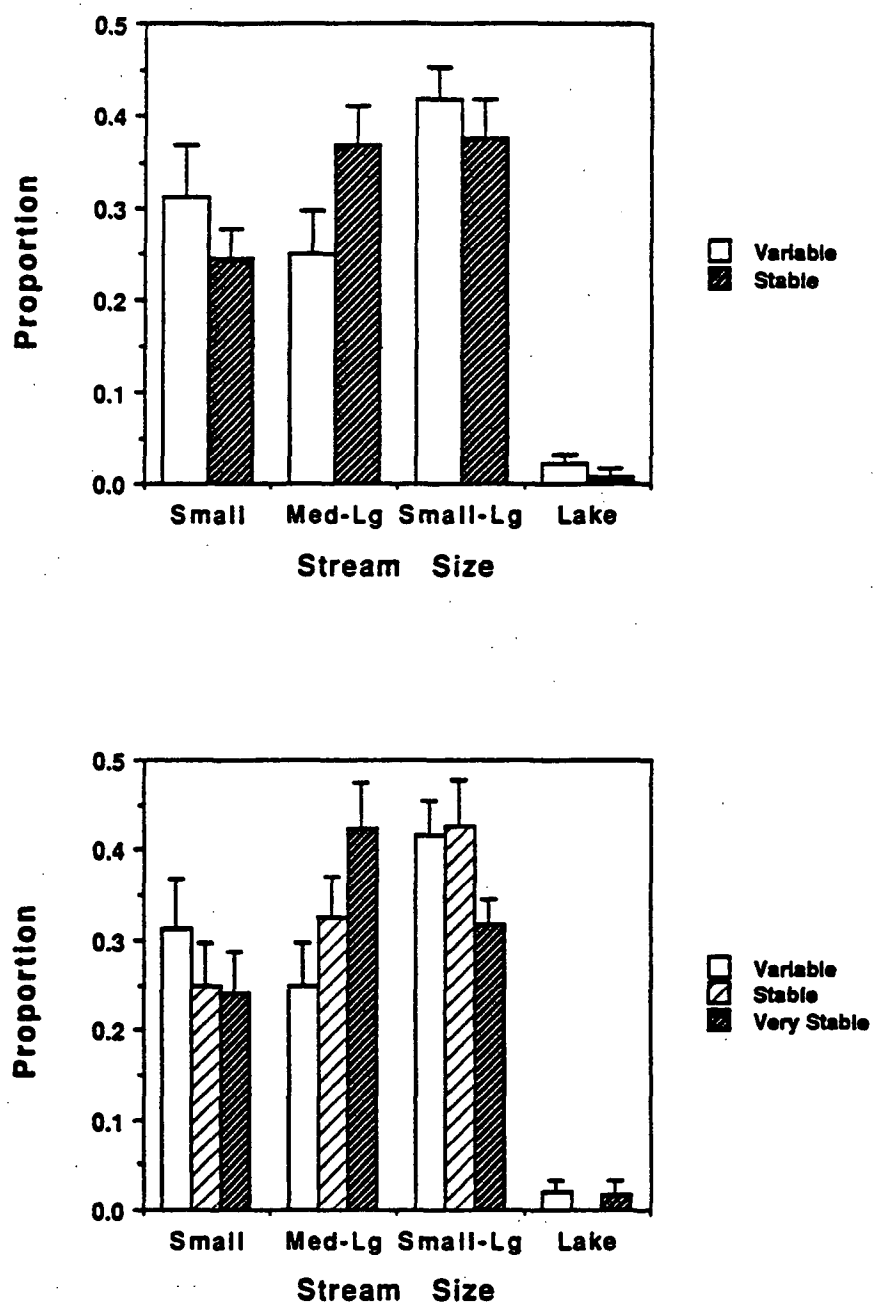Figure 48. Mean group proportions (+ 2se) for 8 trophic categories attributes for the 2-cluster case (upper panel) and 3-cluster case (lower panel). HD = herbivore-detritivore, OM = omnivore, GI = generalist invertivore, SI = surface-feeding invertivore, BI = benthic invertivore, PI = piscivore-invertivore, PL = planktivore, PA = parasite.
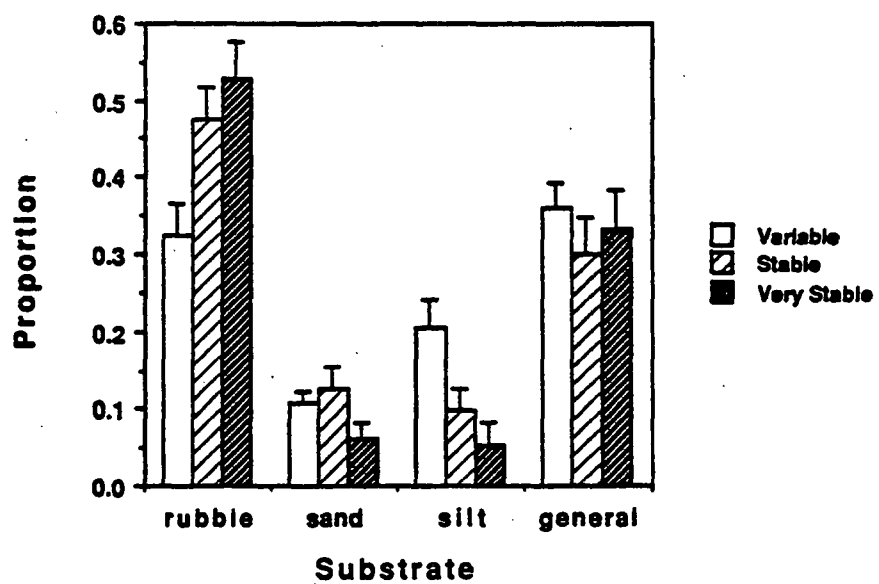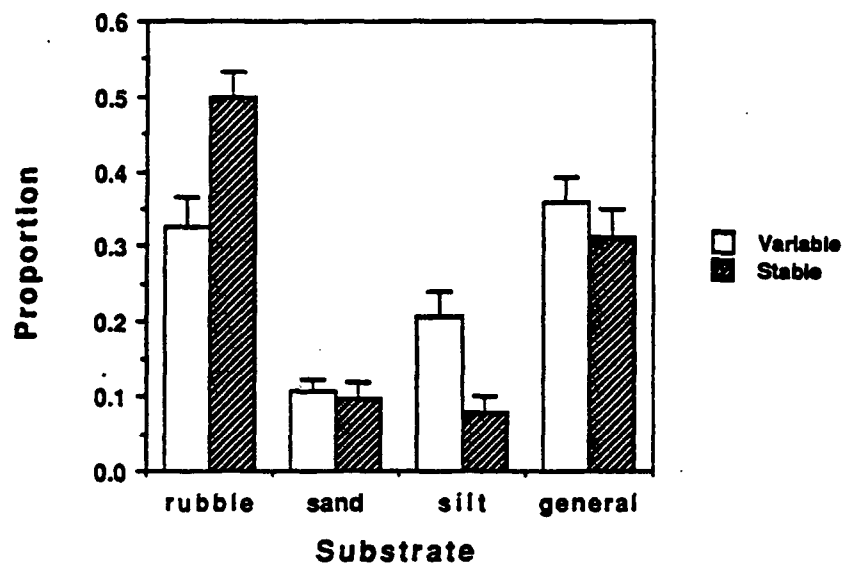
Figure 49. Mean group proportions (+ 2se) for 4 substrate preference
categories for the 2-cluster case (upper panel) and 3-cluster case
(lower panel).

Figure 50. Mean group proportions (+ 2se) for 4 stream size preference categories for the 2-cluster case (upper panel) and 3-cluster case (lower panel).
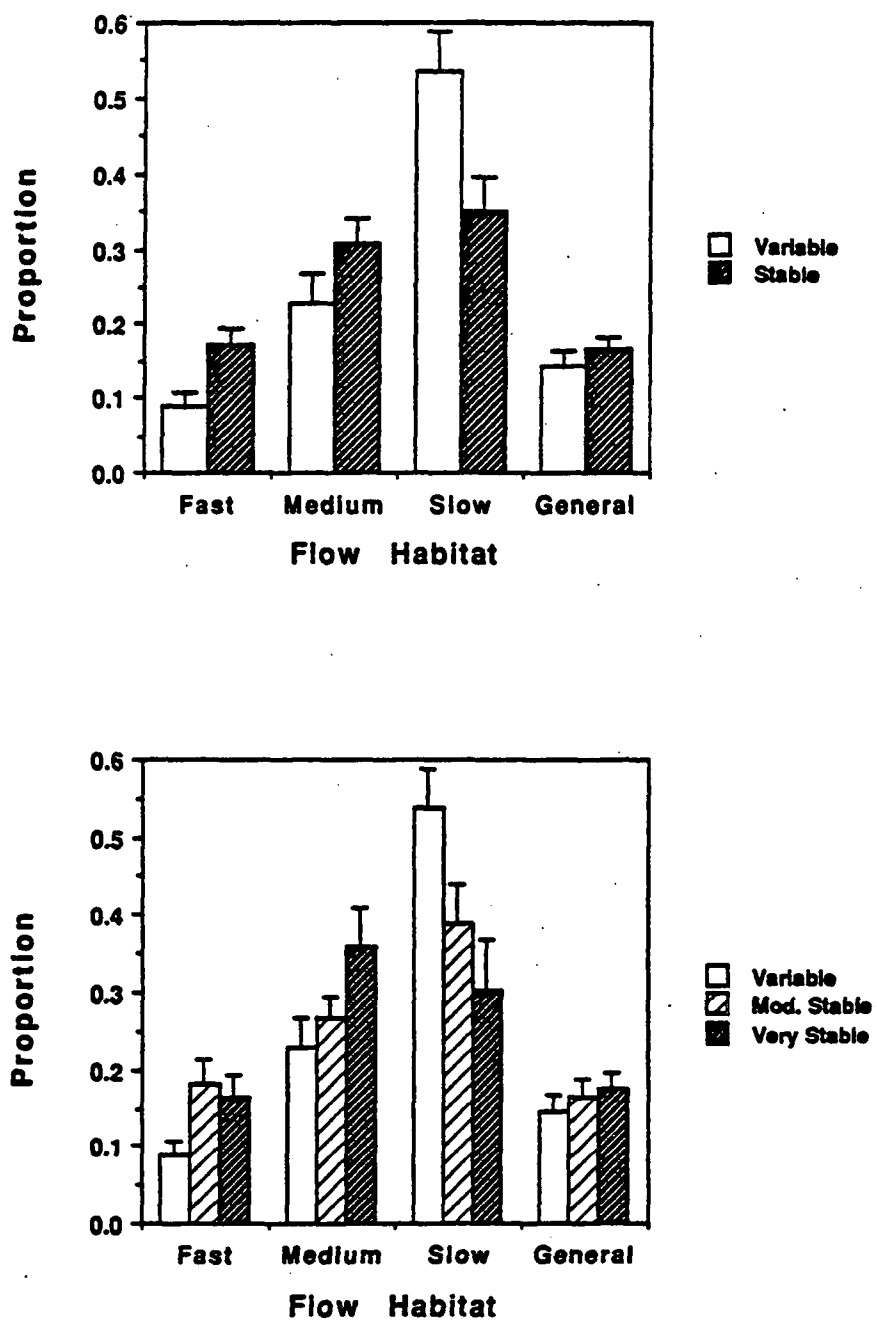
Figure 51. Mean group proportions (+ 2se) for 4 flow habitat categories for the 2-cluster case (upper panel) and 3-cluster case (lower panel).
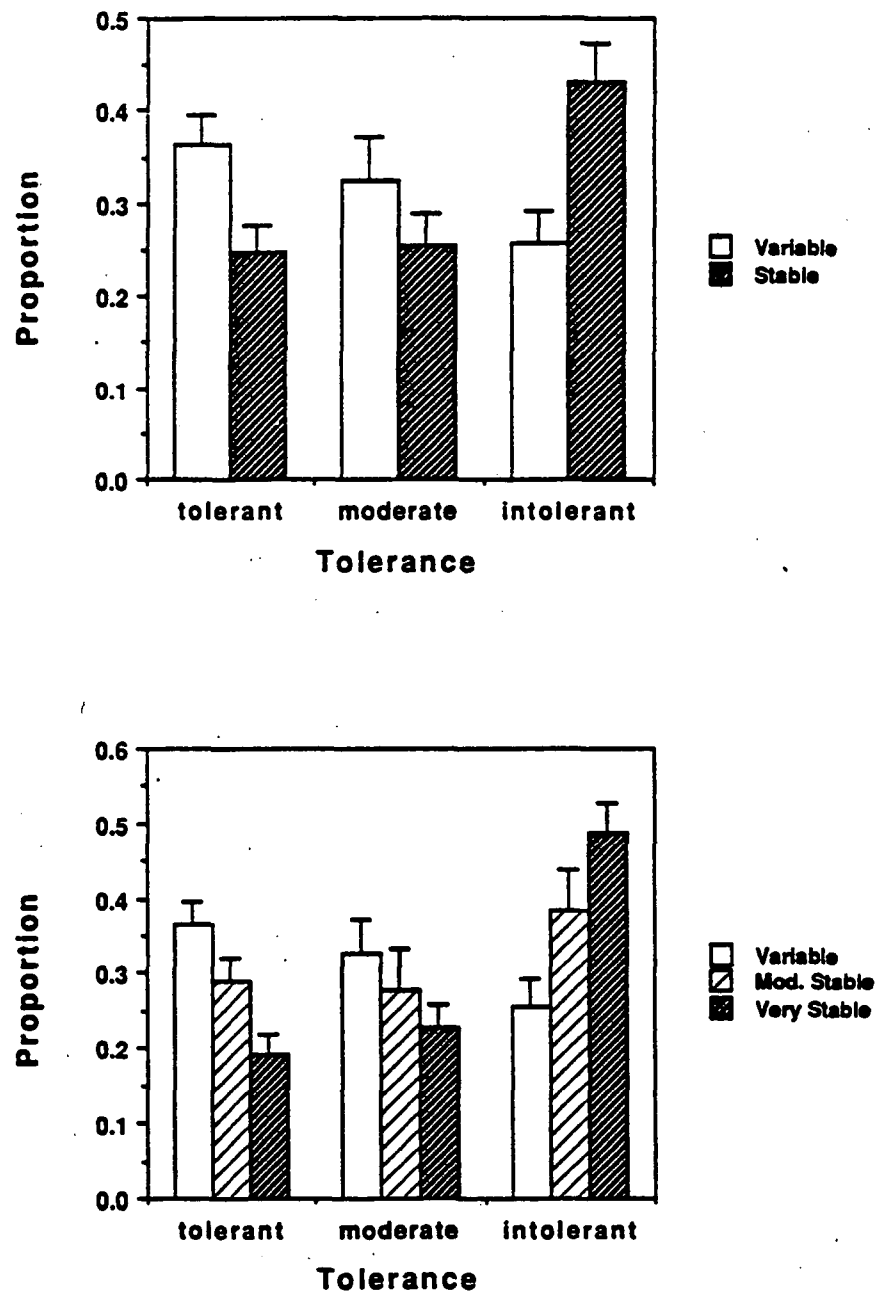
Figure 52. Mean group proportions (+ 2se) for 3 tolerance categories for the 2-cluster case (upper panel) and 3-cluster case (lower panel).