Implications of Streamflow Variability and Predictability for Lotic Community Structure: A Regional Analysis of Streamflow Patterns

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Long-term discharge records (17–81 yr) of 78 streams from across the continental United States were analyzed to develop a general quantitative characterization of streamflow variability and predictability. Based on (1) overall flow variability, (2) flood regime patterns, and (3) extent of intermittency, 11 summary statistics were derived from the entire record for each stream. Using a nonhierarchical clustering technique, nine stream types were identified: harsh intermittent, intermittent flashy, intermittent runoff, perennial flashy, perennial runoff, snowmelt, snow + rain, winter rain, and mesic groundwater. Stream groups separated primarily on combined measures of intermittency, flood frequency, flood predictability, and overall flow predictability, and they showed reasonable geographic affiliation. A conceptual model that incorporates the nine stream clusters in a hierarchical structure is presented. Also, the positions of the 78 streams in a continuous three-dimensional flow space illustrate the wide range of ecologically important hydrologic variability that can constrain ecological and evolutionary processes in streams. Long-term daily streamflow records are a rich source of information with which to evaluate temporal and spatial patterns of lotic environments across many physiographic and ecographic regions. Relative positions of streams in flow space provide a conceptual framework for evaluating a priori the relative importance of abiotic and biotic factors in regulating population and community processes and patterns.

On a analysé des données recueillies chaque jour pendant des périodes prolongées (de 17 à 81 ans) sur 78 cours d'eau du territoire continental des États-Unis en vue d'établir une caractérisation quantitative générale de la variabilité et de la prévisibilité de l'écoulement. On s'est servi de la variabilité générale de l'écoulement, des caractéristiques du régime des crues et du degré d'intermittence pour tirer 11 types de statistiques sommaires de l'ensemble des données recueillies sur chaque cours d'eau. Au moyen d'un technique de groupage non hiérarchique, on a défini neuf types de cours d'eau : courant fort, intermittent, crue éclair, intermittent, ruissellement intermittent, crue éclair, permanent, ruissellement permanent, fonte des neiges, neige et pluie, pluie hivernale et eaux souterraines, conditions moyennes. Essentiellement, on a regroupé les cours d'eau d'après un ensemble de mesures de l'intermittence, de la fréquence et de la prévisibilité des crues et de l'écoulement général, et l'on a constaté une association raisonnable au point de vue géographique. On présente un modèle conceptuel où les neuf groupes sont organisés suivant une structure hiérarchique. Par la position qu'occupent les 78 cours d'eau étudiés dans l'espace d'écoulement tridimensionnel, on peut voir qu'il y a une grande variabilité hydrologique d'importance écologique et que cette variabilité peut restreindre les processus écologiques et évolutionnaires dans les cours d'eau. Les registres quotidiens constitués à long terme sur l'écoulement sont une source d'information précieuse pour l'évaluation de l'environnement lotique en fonction du temps et du lieu dans un grand nombre de régions géomorphologiques et écologiques. La position relative des cours d'eau dans l'espace d'écoulement constitue un cadre conceptuel qui permet d'évaluer a priori l'importance relative des facteurs abiotiques et biotiques dans la régulation des processus et de l'organisation des populations et de la communauté.

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Importance of environmental variability as a factor structuring biological communities has been of long standing interest to ecologists (Hutchinson 1961; Slobodkin and Sanders 1969; Menge and Sutherland 1976, 1987; Wiens 1977, 1984; Connell 1978; Sousa 1984; Pickett and White 1985; Chesson 1986). The extent of variability is often viewed as regulating the relative contributions to community structure of abiotic and biotic processes (e.g. Menge 1976; Menge and Sutherland 1976, 1987; Peckarsky 1983; Wiens 1984) and can serve as an a priori criterion for predicting community pattern and process (Wiens 1984). Stream ecologists are interested in this theory because of the great temporal variability within and between lotic environments, particularly with respect to streamflow. Flow, arguably the most characteristic physical attribute of stream ecosystems, plays a central role in stream ecology (see Hynes 1970). Because streamflow exerts control over many important structural attributes in streams (e.g. habitat volume, current velocity, channel geomorphology, and substratum stability), flow measures represent an integration of complex environmental conditions.

Much recent debate has centered around placing stream communities along some conceptual axis (e.g. equilibrial to nonequilibrial (Wiens 1984)) that corresponds to a physical environmental gradient, often streamflow (e.g. Grossman et al. 1982; Peckarsky 1983; Minshall and Petersen 1985; Reice 1985; Lake and Barmuta 1986; Moyle and Vondracek 1985; Ross et al. 1985, 1987; Angermeier 1987; Heins and Matthews 1987; Matthews 1987; Schlosser 1987; Minshall 1988; Power et al.

1988; Resh et al. 1988). A quantitative description of the variability and temporal predictability of discharge conditions for a set of widely distributed (in space) streams would provide a context for delineating the range of physical environmental variability under which ecological and evolutionary processes operate in lotic habitats. The physical environment could thus be viewed more objectively and a priori predictions of community structure formulated. Such a spatial and temporal perspective of natural environmental variability is lacking not only in stream ecology (Peckarsky 1983; cf. Ward 1989) but in other systems as well (e.g. see Halfpenny and Clark 1988).

In streams, flow fluctuations and extreme conditions such as floods and low or zero flow are primary sources of environmental variability and disturbance, respectively (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 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).

Different combinations of streamflow variation (e.g. range and predictability), patterns of flooding (e.g. frequency and predictability), and extent of intermittency result in different degrees of physical control over biotic organization. Yet, of the limited number of comparative geographical studies, few have considered several mesures of flow variability simultaneously. Consideration of mean flow conditions (Hawkes et al. 1986; Moss et al. 1987; Townsend et al. 1987), variation about the mean flow (Horwitz 1978), and short-term estimates of flood frequency (Cushing et al. 1980, 1983; Minckley and Meffe 1987; Fisher and Grimm 1988) have been used, but only M. Gurtz (in Resh et al. 1988) and Bunn et al. (1986) have incorporated formal measures of temporal predictability (using monthly data) into an analysis. No previous work has used long-term mean daily discharge data to compare flow variability, along with its temporal components, across many spatially-dispersed streams. Given daily data, it is also possible to characterize the temporal components of the disturbance regime, i.e. frequency, timing, and duration of floods and intermittent conditions. Disturbances here are defined according to Sousa (1984, p. 356) as "a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established." Floodplain communities (sensu Welcomme 1979) will not be considered.

The objectives of this paper are to (1) develop an objective and general quantitative characterization of streamflow variability and predictability using long-term mean daily discharge records, (2) analyze flow reords for 78 streams across the continental United States to provide a framework for evaluating the relative variability of any particular stream's physical flow environment, (3) assess hydrologic similarity between streams using components of the flow regime that are of probable ecological significance, and (4) use the results, in conjunction with ecological theory and the limited available empirical data, to suggest possible relationships between hydrologic pattern and population and community level processes and patterns in streams.

Methods

Selection of Streams

The 78 streams chosen for this study (Fig. 1) represented most of the major stream geomorphologic (Brussock et al. 1985), physiographic (Fenneman 1946), and ecographic (Baily 1980; Omernik 1987) regions of the continental United States. Gauged stations were selected from the USGS Water Resources Survey Papers and the entire periods of record (17 to 81 yr) of average daily flow values for all 78 sites were acquired on magnetic tape. We assumed the available records were an unbiased representation of the various streams' flow histories. An attempt was made to include only streams with minimal perturbation (based on the summaries in the Water Survey Papers). For example, excluded streams were those that were impounded or had impounded upstream tributaries, that were channelized, that had more than minimal upstream diversion for irrigation or water supply, or that were similarly impacted. Given the broad geographic distribution of the streams investigated, we used mean annual discharge per unit watershed area, rather than stream order or mean discharge, as an indicator of stream and watershed size (Hughes and Omernik 1983). Summary data for these streams are included in the Appendix.

Derivation of Variables

Daily mean flow values for all stations were read from magnetic tape and analyzed using FORTRAN 5 programs and statistical software packages (MINITAB, BMDP, SPSSX) on a Control Data Corporation CYBER 840 computer. All flow values were transformed by a natural logarithm function ($\ln[x+1]$) so streamflow frequency distributions would approximate a lognormal distribution (see Markovic 1965). Each set of transformed data was then "modularized" by dividing each daily flow value by the grand mean for the period of record (i.e. modularized mean flow = 1.0) for that stream to produce a dimensionless flow index that facilitates comparison between streams (Yevjevich 1972).

Four variables describing stream setting were included in the analysis. Basin area (AREA), mean annual flow (ANNQ), and a size scalar, mean annual flow divided by basin area (Q/AREA), were provided by the Water Survey summaries. The fourth, LNANNQ, was taken as the grand mean flow of the ln-transformed data. These variables are defined in Table 1 and their numerical values for each stream are given in the Appendix.

Three general categories of derived statistics to describe the flow regime were selected for analysis: (1) overall flow variability, (2) pattern of the flood regime, and (3) extent of intermittent conditions. From these three cateogries, 11 summary statistics were derived from the entire record for each stream (Table 1 and Appendix).

Overall flow variability

Three measures of flow variability were used. Mean annual coefficient of variation (ANNCV) assessed overall variability, although it was insensitive to temporal pattern in that it measures only degree of variation about the mean. The predictability aspect of overall flow variation was assessed with Colwell's

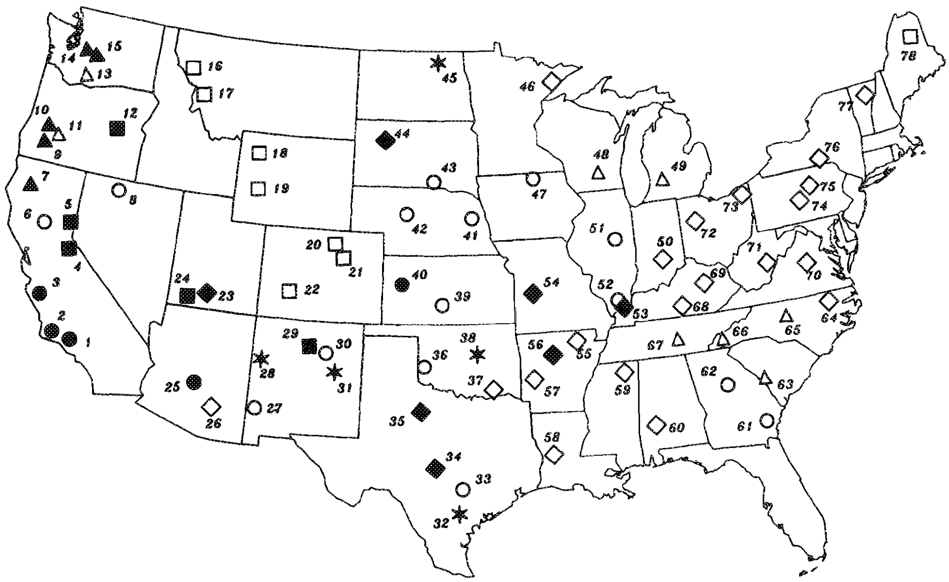

FIG. 1. Location of the 78 streams. Names (by map No.) and summary data are provided in Appendix. Symbols are cluster affiliation and are explained in legend to Fig. 2.

TABLE 1. Definitions for the 15 variables (in four categories) used in the analysis. Refer to text for further details and discussion.

Variable name	Definition
Basin descriptors	
AREA	Contributing watershed area (km^2) above location of stream gauge.
ANNQ	Mean annual flow (m^3·s^{-1}) of untransformed flow values over the period of record.
Q/AREA	ANNQ divided by AREA (mm·yr^{-1}). Size scalar for streams.
LNANNQ	Grand mean flow of the ln-transformed flow.
Overall flow variability	
PREDQ	Colwell's (1974) predictability for all 24-h mean flows over the period of record. ($0<PREDQ<1$)
C/P	Proportion of total predictability (PREDQ) comprised by constancy (C). ($1.0-C/P=$proportion comprised by contingency.)
ANNCV	Mean annual coefficient of variation. The average over all years of the mean flow divided by the standard deviation times 100.
Pattern of the flood regime	
FLODFREQ	Flood frequency (number of floods·yr^{-1})
FLODINT	Median interval (d) between floods.
FLODDUR	Mean duration (d) of floods.
FLOD60D	Index of flood predictability. Maximum proportion of total number of floods over record that occur in any common 60-d period over all years in the period of record.
FLODFREE	Index of flood predictability. Maximum number of 365 d common to all years during which floods have not occurred.
FLODTIME	Median day among all days of the water year (beginning on Oct. 1) on which floods have occurred over the period of record.
Extent of intermittency	
ZERODAY	Average annual number of zero flow days.
LOWFLOW	Average over all years of the annual 24-h low flow value divided by the grand mean flow of the ln-modularized data.

(1974) measure of predictability for periodic phenomena, a measure of temporal uncertainty for some environmental state (here, daily streamflow). Predictability (PREDQ) ranges in value from 0 to 1 and is composed of two additive components: constancy (C), a measure of temporal invariance, and contingency (M), a measure of periodicity. For example, a springbrook with fairly uniform flow may have a predictability value near 1, nearly 100% of which is due to the constancy component (i.e. C/P proportion is high). In contrast, the high predictability of a stream having highly variable flow with a fixed periodicity would be due mostly to contingency. (Refer to Colwell (1974) for a complete description.) In this paper, the environmental state variable (flow) was divided into categories partitioned at 0.1, 0.25, 0.50, 0.75, 1.00 (mean), 1.25, 1.50, 1.75, 2.00, and 2.25 that spanned the entire range of modularized, ln-transformed daily flow values for all streams combined. The temporal unit used was 1 d, i.e. the daily flow state (24-hr mean discharge) for a stream was recorded for each day of a water year. This was repeated for all years of record so that the entire data set for each stream was contained in an 11 discharge category by 365 d matrix. (For leap years, day 366 of the water year (September 30) was deleted.) Each row in the matrix thus summed to the number of years in the record. The selection of a standard temporal unit is arbitrary and will influence the derived predictability values. We chose the daily unit because it allowed utilization of all available information in the record. Also, it was sensitive to sudden flow changes that might otherwise have been obscured by averaging over longer time intervals.

Pattern of the flood regime

Floods occur when flow fills an alluvial channel at bankfull discharge (Leopold 1962; Leopold et al. 1964). This level of flow is usually considered a formative, channel-modifying event (Richards 1982) during which significant substratum movement occurs (both suspended in the water column and moving along the bottom as bed load). We consider significant substratum movement to satisfy objectively Sousa's (1984) criterion for disturbance. Return periods for bankfull discharge can vary from 1–10 yr for different streams depending on basin area,

TABLE 2. Matrix of Pearson correlation coefficients for 15 variables (in four categories) on 78 streams.

	AREA	ANNQ	Q/AREA	LNANNQ	ANNCV	PREDQ	C/P	FLODFREQ
AREA	1.00							
ANNQ	0.04	1.00						
Q/AREA	−0.36[a]	0.40[a]	1.00					
LNANNQ	−0.04	0.84[b]	0.55[b]	1.00				
ANNCV	0.12	−0.39[a]	−0.39[a]	−0.47[a]	1.00			
PREDQ	−0.21	0.34[a]	0.50[b]	0.61[b]	−0.59[b]	1.00		
C/P	−0.12	0.29[a]	0.21	0.49[b]	−0.52[b]	0.64[b]	1.00	
FLODFREQ	0.22[a]	−0.17	−0.38[a]	−0.24[a]	0.31[b]	−0.45[a]	−0.30[a]	1.00
FLODINT	−0.30[a]	0.14	0.41[a]	−0.24[a]	−0.17	0.40[a]	0.12	−0.79[b]
FLOD60D	−0.06	−0.07	0.10	−0.03	0.04	0.29[a]	−0.20	−0.16
FLODFREE	−0.02	−0.14	0.09	−0.08	0.04	0.23[a]	−0.12	−0.02
FLODDUR	0.10	−0.15	−0.15	−0.14	0.04	0.22[a]	0.00	−0.01
FLODTIME	0.28[a]	−0.19	−0.55[b]	−0.19	0.31[a]	−0.09	−0.09	0.05
ZEROFLOW	0.21	−0.32[a]	−0.32[a]	−0.31[a]	0.92[b]	−0.36[a]	−0.29[a]	0.22
LOWFLOW	−0.15	0.34[a]	0.38[a]	0.57[b]	−0.81[b]	0.48[b]	0.79[b]	−0.34[a]

	FLODINT	FLOD60D	FLODFREE	FLODDUR	FLODTIME	ZEROFLOW	LOWFLOW
FLODINT	1.00						
FLOD60D	0.20	1.00					
FLODFREE	0.04	0.75[b]	1.00				
FLODDUR	−0.06	0.58[b]	0.40[a]	1.00			
FLODTIME	−0.04	0.20	0.14	0.28[a]	1.00		
ZEROFLOW	−0.10	0.08	0.03	0.10	0.21	1.00	
LOWFLOW	0.22[a]	0.08	0.11	0.13	−0.11	−0.61[b]	1.00

[a]p<j0.05.
[b]p<0.01.

sediment character, basin geomorphology, channel slope, and channel entrenchment (Richards 1982). However, the associated return periods for the discharge level effective in moving the greatest quantity of substratum range in the briefer interval of 1–3 yr (Richards 1982). Therefore, the effective flow for moving substratum is generally less than or equal to bankfull discharge. Leopold et al. (1964) give the average return period for bankfull discharge as 1–2 yr, which results in an average return time of 1.5 yr, a figure often used (e.g. Newbury 1984). We chose to use a more conservative flood value corresponding to a return period of 2 yr for the bankfull discharge.

Flood-level flow was calculated for each stream as follows. Annual 24-hr peak flows for the entire period of record were ranked and plotted on lognormal probability paper (using MINITAB) and a coefficient of determination (r^2) calculated for the regression line (cf. Morisawa 1968). The flow value corresponding to the 50% exceedence probability (2-yr return interval) was then chosen as the threshold flood value for that stream. Division by the grand mean modularized the value. The high r^2 values resulting from this analysis (Appendix) justified the use of the lognormal versus other distributions (see Richards 1982). An important assumption we made was that all flows exceeding these threshold flood values were qualitatively similar because the streams were at "bankfull discharge," i.e. the energy associated with the additional flow was expended outside the channel. (It is also important to note that use of annual mean 24-hr peak flow rather than instantaneous flow in the ranking procedure results in a consistent underestimation of actual bankfull discharge. This will be particularly true for streams that flood for only minutes during a day (e.g. see Minckley and Meffe 1987). However, because available long-term daily flow records consist of 24-hr means, rather than instantaneous values, it is necessary to define floods using the peak 24-hr mean. This technique thus measures an index of bankfull discharge.)

After establishing a threshold value for a stream-specific flood-disturbance, the flood regime for the entire period of record was evaluated with respect to six derived variables (Table 1). Flood frequency (FLODFREQ) was the mean number of floods per year over the period of record. Floods lasting more than 1 d counted as one flood. The intervals in days between floods were computed and the median determined (FLODINT). When the interval between two consecutive floods was 2 d or less, the floods were typically combined into one event. For those streams having floods clearly resulting from seasonal snowmelt (based on observation of the timing and duration of all floods in the record), the cutoff interval was relaxed to 8 d because flow conditions during these intervals were high but just below the prescribed flood threshold value. The mean duration for floods (FLODDUR), a possible index of disturbance intensity, was calculated by considering how many days each flood lasted. The predictability of flooding was assessed with two indices. By determining the day of the water year (October 1–September 30) on which each flood occurred, the temporal distribution of floods in a stream could be evaluated. The maximum proportion of all floods falling in any 60-d period common to all years in the record was determined to provide an index of flood predicatability (FLOD60D). Similarly, the maximum number of 365 d over all water years during which no floods occurred (FLODFREE) also characterized predictability of flooding. An index of seasonality (FLODTIME) was considered by determining the median day (of the water year) among all days on which floods occurred over the entire period of record.

Extent of intermittent conditions

Intermittency was evaluated by determining the average annual number of zero flow days for each stream (ZERODAY).

TABLE 3. Numerical means and standard deviations (in parentheses) of 11 variables for nine clusters.

	Harsh intermittent[a]	Intermittent flashy	Intermittent runoff	Perennial flashy	Perennial runoff	Winter rain	Snow + rain	Snowmelt	Mesic groundwater
ANNCV	151.3	88.3	68.2	24.2	31.4	20.7	26.4	27.5	10.5
	(37.4)	(25.9)	(22.0)	(11.9)	(7.5)	(8.6)	(11.2)	(9.3)	(6.1)
PREDQ	0.29	0.24	0.25	0.49	0.44	0.67	0.56	0.69	0.72
	(0.07)	(0.07)	(0.06)	(0.17)	(0.09)	(0.11)	(0.11)	(0.11)	(0.08)
C/P	0.54	0.30	0.32	0.80	0.69	0.70	0.66	0.61	0.89
	(0.20)	(0.11)	(0.13)	(0.14)	(0.12)	(0.11)	(0.14)	(0.13)	(0.08)
FLODFREQ	0.87	1.21	0.81	1.01	0.75	0.77	0.86	0.69	0.63
	(0.12)	(0.07)	(0.08)	(0.14)	(0.09)	(0.11)	(0.09)	(0.08)	(0.09)
FLODINT	263	47	342	144	304	299	263	361	414
	(62)	(14)	(81)	(85)	(71)	(106)	(105)	(15)	(104)
FLOD60D	0.59	0.61	0.55	0.46	0.48	0.65	0.74	0.94	0.51
	(0.09)	(0.09)	(0.15)	(0.07)	(0.11)	(0.09)	(0.05)	(0.07)	(0.08)
FLODFREE	124	192	136	132	101	226	172	273	131
	(65)	(36)	(66)	(56)	(49)	(49)	(33)	(53)	(35)
FLODDUR	2.5	2.3	2.3	3.0	1.6	1.9	12.7	7.2	2.2
	(2.0)	(0.4)	(1.6)	(1.8)	(0.6)	(0.4)	(3.1)	(3.3)	(1.7)
FLODTIME	236	159	207	211	163	99	209	242	149
	(45)	(64)	(34)	(50)	(22)	(16)	(27)	(17)	(41)
ZEROFLOW	96.2	32.6	17.0	0.1	0.1	0	0.2	0	0
	(17.0)	(16.3)	(11.4)	(0.4)	(0.4)	(0)	(0.4)	(0)	(0)
LOWFLOW	0.02	0.10	0.14	0.61	0.45	0.66	0.46	0.66	.83
	(0.02)	(0.05)	(0.12)	(0.20)	(0.14)	(0.16)	(0.13)	(0.09)	(0.08)

[a]Scores exclusive of Mauvis Coulee, North Dakota, which was added a posteriori to this group.

An additional index of intermittency (LOWFLOW) was calculated as the mean of all the annual low flow values divided by the grand mean discharge. Thus, streams with potentially biologically significant low flow periods that approached but did not reach zero were assessed by this variable.

Analysis and Results

Cluster Analysis of Streamflow Pattern

One objective of the analysis was to determine similarities with respect to flow regime among the 78 streams. A descriptive cluster analysis approach that was exploratory and made no distributional assumptions that would justify statistical inferences was adopted. Because we were interested in examining similarity between streams based on variables derived from the daily flow records, the four basin descriptors (AREA, ANNQ, Q/AREA, and LNANNQ) were deleted from the cluster analysis (but see below for a check on this procedure).

First, inspection of all pairwise plots of variables across all streams revealed that the relationships between almost all pairs were no higher than first-order. Therefore, the strengths of linear association among variables were assessed (on BMDP) using Pearson correlation coefficient, r (Table 2). Many of the derived variables were significantly correlated with one another, due both to the large sample sizes and the inherent interdependency between flow-related variables. However, the generally low r values in Table 2 indicate that much variability existed in the relationship between most variables. For example, PREDQ and ANNCV, temporal and nontemporal measures of overall flow variability, respectively, correlated differentially with measures of the flood regime. Both variables showed some association with flood frequency (FLODFREQ and FLODINT), but only PREDQ showed nonzero correlation with the other aspects of the flood regime, viz. flood predictability (FLOD60D and FLODFREE) and flood duration (FLODDUR). Thus, single measures of overall flow variability (i.e. PREDQ and ANNCV) generally could explain very little of the variability in flood disturbance characteristics.

For the cluster analysis, a nonhierarchical classification scheme (BMDP K-means) was utilized. Nonhierarchical clustering was a useful approach for exploring initial relationships between samples (here, streams) that shared similarities in measured characteristics (here, 11 derived streamflow variables) (Gauch 1982). Because resultant clusters had no joint structure, statistical inferences concerning differences between clusters were not appropriate. However, cluster designations suggested hypotheses that could be subjected to additional multivariate techniques (Gauch 1982). Values of the 11 derived streamflow variables for each stream were used as input. Because of the differences in the magnitudes in the units, variables were standardized by dividing the value of each variable by the standard deviation of that variable. The classification routine assigned each sample (stream) to one of the K user-defined clusters based on minimum Euclidean distance (in variable space) between the sample and the centers of all clusters. The number of clusters specified in nonhierarchical cluster analysis was arbitrary. After several runs, we chose nine clusters because this number optimized group separation and interpretation. Table 3 gives the cluster mean and standard deviation for each variable for each of the nine groups.

The nine clusters could be grouped broadly into intermittent and perennial streams. Among the former, harsh intermittent streams were characterized by long periods of zero flow and by very low flow each year. They tended to occur in the arid to semi-arid southwest (Fig. 1), with the exception of one stream, which was placed a posteriori into the harsh intermittent group (see Table 3, Appendix). Streams with long periods of intermittency could, however, also occur in more mesic, eastern regions (see Williams and Hynes 1976; Delucchi 1988). Two additional groups of intermittent streams had a moderate degree of zero flow and low flow conditions. Intermittent flashy streams had a high frequency of floods that were moderately seasonal in their distribution. They occurred generally in the arid southwest, where vegetation cover in the watersheds is sparse and precipitation is seasonal. Members of the intermittent runoff group were located in the more semi-arid central United States. They flooded less frequently and less predictably, perhaps due to relatively more watershed vegetation cover and less seasonal precipitation patterns. All three groups of intermittent streams were characterized by high variability and low predictability of flow.

Perennial streams had no more than occasional zero flow days (Table 3). The perennial flashy group was characterized by a high frequency of nonseasonal flooding. They tended to occur in the arid to semi-arid regions of the United States and to be maintained by subsurface flow (note low ANNCV and high C/P in Table 3). Perennial runoff streams, which generally occurred in the more heavily-vegetated, mesic regions (Fig. 1), flooded less frequently and appeared to be less influenced by subsurface flow. The one desert stream in this group shared similar temporal characteristics (e.g. PREDQ, FLOD60D, FLODFREE — see Appendix) with the geographically proximate intermittent flashy group, but its flow constancy (e.g. C/P, LOWFLOW) imparted characteristics that caused it to cluster differently.

The winter rain streams of the Pacific Northwest were characterized by intermediate flood frequency and medium to high seasonality of flow and flooding. The median time for floods (FLODTIME) in this group was day 99 or early January (Table 3). The mesic groundwater streams, most temporally constant of all groups with respect to flow variation, were similar to the winter rain streams except that they flooded relatively infrequently and less seasonally than did the latter. They were generally eastern in distribution, with the exception of two Pacific Northwest members, one of which was actually a lake outlet stream and thus had high flow constancy and lower flood frequency (see Appendix).

The final two groups were clearly influenced by seasonal snowmelt. Snowmelt streams flooded very predictably; however, depending on annual snowpack and vernal weather conditions, they did not necessarily flood every year. They had low variability and high predictability of flow. All but one were western montane systems. The snow + rain group also consists of western montane streams that differ from the previous group in their greater flood frequency, lesser (but still relatively high) flood predictability and lesser flow predictability. These watersheds appeared to be influenced not only by annual snowfall, but by seasonal rainfall patterns as well. Interestingly, flood duration (FLODDUR) was high for these two stream groups (Table 3), but for no others. This variable, therefore, did not provide additional separation between stream types.

Streamflow Clusters versus Alternative Variables

To address the possibility that the nine clusters could have been described from the four discarded basin descriptors, a MANOVA ($k=9$ clusters, $p=4$ variables, $n=78$ streams) was run on SPSSX. Although the correlation between the individual basin descriptors and each of the 11 derived streamflow variables was generally low (Table 2), the inherent correlation structure between these four variables and the original 11 restricted hypothesis tests of mean differences between clusters (i.e. because clusters were generated using variables correlated to these four). However, analysis of variance could be used to describe (as opposed to test) the differences between the established clusters with respect to the four variables (P. Chapman, Department of Statistics, Colorado State University, pers. comm.). Computed statistics and associated p-values could be used to suggest differences between groups. In the MANOVA each of the 78 streams was coded according to its cluster affiliation. Using AREA, Q/AREA, ANNQ, and LNANNQ as variables, the established clusters appeared to differ with respect to the four basin descriptors (Wilk's $\lambda=0.42$, $p<0.001$). Examination of the univariate F-tests further suggested that Q/AREA was the only variable responsible for the difference between clusters ($F=3.94$, $p<0.001$). Visual inspections of central tendency and range of values for Q/AREA in each established cluster revealed that winter rain streams had very high values, harsh intermittent streams had very low values, and all other stream categories were intermediate and overlapping in value. (This same trend, though less pronounced, was observed for LNANNQ and ANNQ as well.) In conclusion, the four discarded basin variables could not satisfactorily separate the 78 streams into the nine clusters established from the derived streamflow variables.

Discussion

Implications for Community Structure

Disturbance (floods and intermittency) and flow variability interact to provide a complex physical template (sensu Southwood 1977, 1988) that can influence population and community patterns of stream organisms. Clearly, the relative contributions of these hydrologic variables to the overall selective forces in streams are themselves temporally variable and thus conceptually difficult to disentangle. The recognition that streamflow environments are more appropriately considered as arrayed continuously along axes of hydrologic variability, not as discreet units or clusters, further emphasizes this point. Some combination of flood frequency (FLODFREQ and FLODINT), flood predictability (FLOD60D and FLODFREE), and overall flow variability (temporal PREDQ or nontemporal ANNCV) are likely contributors to the physical templates in all but the harsh intermittent streams. Therefore, these hydrologic components can be argued to interact to establish a significant portion of the gross physical flow template in most streams (and thereby to delimit the range of biotic responses and interactions). By viewing all 78 streams in the space generated by these three components (Fig. 2), a sense of the range of ecologically important hydrologic variability for a large number of North American streams is achieved. (Although this representation excludes the intermittency axis, note that intermittent streams are included in the figure.

To assess the relative contributions of various components of streamflow variability to a stream's physical flow template, a conceptual model that incorporates the nine clusters can be constructed (Fig. 3). Hydrological variables can be hierarchically ranked as follows, according to the order of their importance in defining a stream's flow template: degree of intermittency, flood frequency, flood predictability, and overall flow predictability/variability.

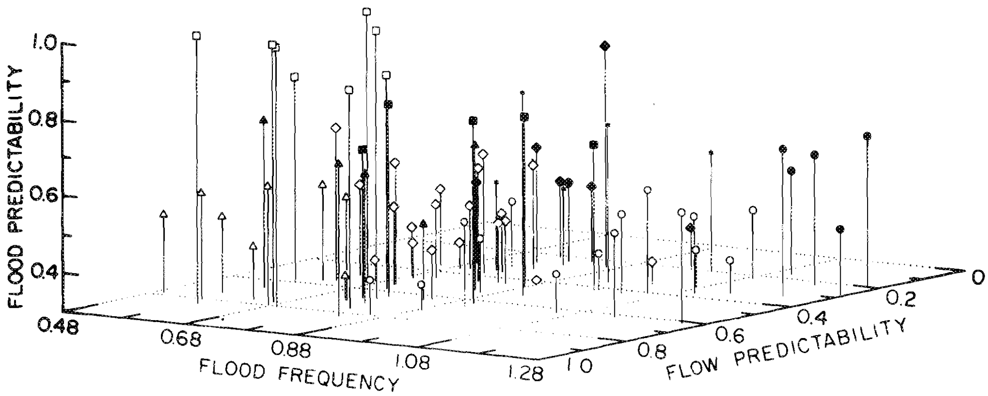

FIG. 2. Plot of the 78 streams (coded by cluster) showing wide distribution in three-variable space defined by flood frequency (FLOD-FREQ), flood predictability (FLOD60D), and overall predictability of flow (PREDQ). Note that intermittent streams are included though an intermittency axis is excluded. (★ = harsh intermittent, ● = intermittent flashy, = intermittent runoff, ○ = perennial flashy, ◇ = perennial runoff, ▲ = winter rain, □ = snowmelt, ▪ = snow + rain, Δ = mesic groundwater.)

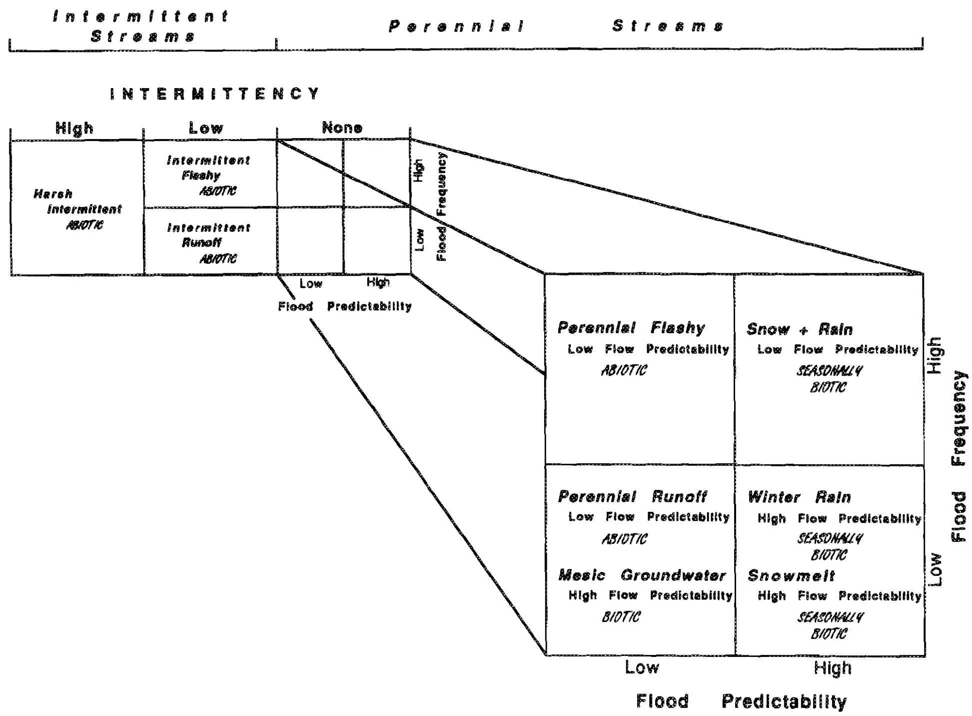

FIG. 3. Conceptual model of classification of stream clusters based on hierarchical ranking of four temporal components of discharge regime. The degree of intermittency is the first variable of consideration. For streams with low intermittency and for perennial streams, flood frequency is a variable separating stream types. For perennial streams flood predictability must also be considered. Overall flow predictability (irrespective of disturbance regime) is generally important only within certain combinations of flood frequency and predictability in perennial streams. Combinations of hydrologic variables result in streamflow templates in which the relative contributions to community structure of abiotic and biotic processes are expected to differ, as indicated. See text for more complete discussion.

The premise underlying the following discussion is that highly variable and/or unpredictable flow regimes provide a physical template in which abiotic processes are of predominant importance in controlling lotic processes and contributing to observed ecological patterns, whereas more benign or predictable flow environments are conducive to the development of stronger biotic interactions such as competition or predation, which can directly influence observed pattern (cf. Sanders 1969; Fisher 1983; Peckarsky 1983; Ward and Stanford 1983; Reice 1985; Ross et al. 1985; Walde 1986; Resh et al. 1988). However, in many if not most lotic systems, streamflow regimes are intermediate between these extremes such that both abiotic and biotic factors contribute to community structure at various times (Matthews 1988; Minshall 1988; Power et al. 1988; also cf. Menge and Sutherland 1987; Southwood 1988).

Ecological attributes that reflect streamflow environment are considered at the population and community levels of organization. Life history characteristics and other population

TABLE 4. Potential biological attributes in lotic habitats as four independently-considered hydrological factors increase in magnitude. See text for further development and appropriate references.

Hydrologic factors	Biological attributes: Population	Biological attributes: Community
Intermittency	Inverts: Diapause/aestivation Desiccation avoidance behavior Increasing dispersal capability Fish: Small body size Upstream migrations following resumption of flow Increased physiological eurytopy	Trophically simple Richness: Low relative to regional species pool Stability and persistence: High due to drought-selected taxa Succession: Autogenic forces predominant (due to seasonal flow reduction) High predictability of trajectory after resumption of flow Community Structure: Abiotic factors predominant
Flood frequency	Inverts: Small body size Accelerated and asynchronous development Behavioral avoidance of floods Fish: Small body size Fusiform shape favored Behavioral avoidance of floods Low recruitment, uneven age distribution	Trophically simple Richness: Low relative to regional species pool Stability and persistence: Increases due to flood-selected taxa Succession: Allogenic forces predominant Poor development following floods; limited species replacements Community structure: Abiotic factors predominant
Flood predictability	Inverts: Increased developmental synchrony Emergence/reproduction temporally cued to flood(s) Fish: Larger body size, more specialists Behavioral and/or life history avoidance of floods High recruitment, more even age distribution	Trophically complex Richness: Intermediate relative to regional pool Stability and persistence: Increases due to flood-adaptations Succession: Autogenic forces predominant; increasing predictability of trajectory Community structure: Biotic factors predominant seasonally
Flow predictability	Inverts: Larger body size, more specialists Increasing proportion long-lived species Developmental synchrony variable Fish: Larger and more specialists Increasing proportion of long-lived species High recruitment, more even age distribution	Trophically complex Richness: High relative to regional species pool Stability and persistence: Decreases due to flood-prone species Secondary succession: Autogenic forces predominant Strong development following floods; timing of flood yields unpredictable path Community structure: Biotic factors predominant

characteristics can vary within the same species inhabiting qualitatively different habitats as a function of habitat-related selective forces (Tinkle and Ballinger 1972; Southwood 1977; Hornbach and Childers 1986; Petranka et al. 1987; Willows 1987; see also Begon et al. 1986, chapter 14). Moreover, there is an increasing body of evidence suggesting local population adaptation not only to absolute environmental variables but to the degree of environmental variation as well (Nichols et al. 1976; Leggett and Carscadden 1978; Vepsäläinen 1978; Diamond 1982; Dingle 1984; McLachlan 1985; Kaitala 1987; Etter 1988). Qualitative trends toward some local optimum life history attributes within species' adaptative constraints (cf. Levins 1968) may be observable, particularly for local populations inhabiting streams of differing flow patterns within relatively close geographic proximity. At the community level, persistence and stability (sensu Connell and Sousa 1983) and succession (sensu Fisher 1983) are considered.

The following discussion is largely speculative given the virtual absence of empirical data on stream organisms that correspond to the available long-term flow data. It is intended primarily to suggest possible fruitful areas of focus in relating hydrological pattern to ecological process and pattern (see Resh et al. 1988 for other speculative suggestions). The summary in Table 4 should be referred to throughout the discussion.

Streams that experience prolonged periods of intermittency (e.g. harsh intermittent) present special physiological and life history problems to the flora and fauna when compared with perennial streams. Long periods of zero flow conditions may provide selective pressure for specific life history characteristics such as invertebrate aestivation and egg diapause (Williams and Hynes 1977), high vagility among fishes (Larimore et al. 1959), and physiological tolerance to low dissolved oxygen (Williams and Hynes 1977; Matthews 1987) and may eliminate poorly-adapted colonizing taxa (Delucchi 1988). These characteristics may lead to such community attributes as high persistence and stability and relatively high predictability of successional patterns following the seasonal resumption of flow (Table 4), although these attributes can vary depending on the duration of drying, the time since drying and the distance from recolonization sources (cf. Iversen et al. 1978; Delucchi 1988, 1989). Other hydrological characteristics (flood frequency, flood predictability, overall flow predictability) should be of secondary importance in these streams. In general, biotic interactions should contribute relatively little to community structure given the demanding environment.

As intermittency becomes less prolonged (e.g. in intermittent flashy and intermittent runoff streams), other hydrologic forces such as floods become increasingly important in influencing community structure (cf. Stehr and Branson 1938; Harrel and Dorris 1968). Floods are widely viewed as reset mechanisms (Fisher 1983; Cummins et al. 1984; Minshall et al. 1985b; Resh et al. 1988), and flood-related mortality to lotic organisms can result either directly from scouring, crushing, or downstream export of individuals (e.g. Thorup 1970; Power and Stewart 1987; Minckley and Meffe 1987) or indirectly from food resource loss (Hanson and Waters 1974). In streams that both flood frequently and dry annually, animals may possess life history characteristics for both flood and desiccation avoidance. For example, insects of Sycamore Creek in Arizona have presumably adapted to the flood regime of high frequency through accelerated developmental rates that reduce the time larvae spend in the stream and that allow adults to recolonize quickly through oviposition following flooding (Gray 1981; Fisher et al. 1982). Rapid development and habitat selection by ovipositing adults enhance persistence through intermittent conditions. Trends toward increased developmental rate, decreased developmental synchrony, and reduced body size may be generalized responses of aquatic insects to increasing disturbance frequency (cf. Slobodkin 1968), particularly in warmer climatic regions where aerial adults can survive year-round. Also, in warm-water streams subject to both intermittency and frequent flooding, succession following disturbance can be pronounced for rapidly-reproducing species such as algae and insects (Fisher et al. 1982). In such systems, time since last flood can help explain community structure as well (Fisher and Grimm 1988). Because of life history adaptations to the disturbance regime (cf. Fisher et al. 1982) community persistence can also be high in such streams.

Where streamflow is perennial (i.e. the remaining six clusters), components of the flood regime, particularly the interaction of frequency (FLODFREQ and FLODINT) and predictability (FLOD60D and FLODFREE) are likely of primary significance in structuring lotic communities. If flood frequency is high, the relative contributions of biotic interactions to community structure are likely to depend on the temporal pattern of the flood regime. Overall flow predictability (PREDQ) and variability (ANNCV) are likely to attain relative importance in describing a stream's flow template only under certain combinations of flood frequency and flood predictability (Fig. 3). As flood frequency increases, selection pressure is presumably exerted for certain behavioral and life history characteristics that maintain population persistence or homeostasis (cf. Slobodkin 1968) (see Table 4). For example, some invertebrates actively migrate either into the substratum (Zahar 1951) or to quieter backwaters (Lehmkuhl and Anderson 1972) to avoid spates. Fish avoidance behavior may reflect evolutionary history with frequent floods (Meffe 1984). Populations from streams with high flood frequency can be characterized by small, vagile and/or colonizing assemblages of invertebrates (e.g. Siegfried and Knight 1977) and of fish (e.g. Harrell 1978; Schlosser 1985, 1987; Meffe and Minckley 1987). The population densities of such species can fluctuate as a response to floods, but persistence can be high (e.g. Matthews 1986; Meffe and Minckley 1987; Meffe and Berra 1988). The most persistent fish species are likely to be those possessing a morphology favorable to surviving flood flows (e.g. Schlosser 1985; Matthews 1986; Minckley and Meffe 1987). Floods have been shown to regulate community structure by facilitating local coexistence between asymetrically-competitive algal species (Power and Stewart 1987) and invertebrate species (Hemphill and Cooper 1983; McAuliffe 1984) and between an exotic fish predator and its native, relatively flood-resistant prey (Meffe 1984).

The importance of high flood frequency can be tempered somewhat by high flood predictability because of potential, evolutionary-mediated life history adjustments to this predictability (Huston 1979; Thiery 1982) (Table 4). Moyle and Vondracek (1985) suggested that the high predictability of nonflood periods in montane western streams serves as a reliable environmental cue for native salmonid species, whose flood-susceptible fry are present only during the flood-free summer season. Similarly, John (1963, 1964) found that cyprinid life histories in the desert southwest are linked to the timing of floods, which can be used as reproductive cues. Gray (1981) suggested that some insects' reproductive activities may be adjusted to a largely seasonal flood regime.

Conditions of high flood frequency and low flood predictability (e.g. in perennial flashy streams), are likely to minimize the contributions of biotic interactions to community structure over long time scales. However, in years when periods between floods are long and overall flow conditions are relatively invariant (see C/P in Table 3), biotic interactions might become sporadically important, particularly for species with short generation times. Brier Creek, a perennial stream in southern Oklahoma with late summer low flow, perhaps falls into this category. Extensive research on this system has shown that floods are an important structuring agent in this stream, but that biotic factors such as competition and predation can also contribute to community structure during periods of flow constancy (reviewed in Matthews 1988).

Where high frequency is coupled with relatively high predictability of flooding (e.g. snow + rain streams) biotic interactions should attain relative importance, at least seasonally between floods (cf. Minshall et al. 1985a; Moyle and Vondracek 1985). Although floods typically occur in late spring in snow + rain streams (see FLODTIME in Table 3), in some years winter rains cause severe early season flooding (Erman et al. 1988). Winter floods in Sagehen Creek tend to reduce egg survival and adult densities of native brook trout (and sculpins) (Erman 1986; Erman et al. 1988), to such an extent that fry of nonnative, spring-spawning rainbow trout are able to compete successfully with brook trout fry in the late spring (Seegrist and

Gard 1972). However, because the flood-free season is long and coincides with the period of recruitment and growth, fish assemblage persistence and stability can be high on a year-to-year basis in these and other snowmelt streams (Moyle and Vondracek 1985; Erman 1986). (Interestingly, intermittent flashy streams are also characterized by a high flood frequency and a moderately high flood predictability (Table 3). Biotic interactive strength might therefore be enhanced during the flood-free season; however, this season is coincident with the period of stream intermittency, which would minimize the contributions of biotic interactions to community structure).

For streams with low flood frequency, the importance of biotic interactions may reflect not only flood predictability, but overall flow predictability/variability as well. Snowmelt and winter rain streams have relatively high flood predictability (Table 3, Fig. 3) and thus would be expected to provide environments conducive to the expression of strong biotic interactions, at least seasonally (cf. Minshall et al. 1985a). The relatively high overall flow predictability (low variability) in these streams should further enhance this expression (Table 4). Succession in these streams should be relatively predictable given the seasonal nature of the flood regime.

Perennial runoff and mesic groundwater streams have typically low flood predictability coupled with low flood frequency, but they differ from one another with respect to overall flow predictability (Table 3, Fig. 2). Perennial runoff streams generally have low overall flow predictability; therefore, abiotic processes are likely to predominate in such lotic systems. High flow variability can reduce the consistency of biotic interactions by frequently upsetting current-related resource and microhabitat distributions (Reice 1985; Schlosser and Toth 1984; Bain et al. 1988; Power et al. 1988) and perhaps by requiring individuals to make physiological adjustments to changing physico–chemical conditions (cf. Slobodkin 1968; Slobodkin and Sanders 1969). However, during periods of low flow, and the attendant reduction of habitat area or volume, biotic interactive strength could become temporarily important (cf. Matthews 1988), particularly if habitat reduction and crowding were not so great as to induce physiological and behavioral stress. Succession in these streams is not likely to be strongly developed or detectable due to the relatively unpredictable and variable nature of the flow regime (cf. Fisher and Grimm 1988). Community persistence, however, may be great given the presumed adaptedness of the fauna to environmental variability (cf. Matthews 1986). (Intermittent runoff streams, slightly more variable than perennial runoff streams and with only a few zero flow days per year (Table 3, Fig. 3) might also exhibit these characteristics).

Mesic groundwater streams flood relatively infrequently and have very high overall flow predictability due largely to flow constancy (Table 3). Strong biotic interactions and successional patterns should be relatively well-developed in such streams (cf. Fisher 1983) (Table 4). However, these streams should also be relatively vulnerable to disturbance from temporally unpredictable floods. If, for example, a stream has not been flooded for a long time, "late-succesional" species can show low resilience (e.g. Harrell 1978) or species in vulnerable life history stages (e.g. Thorup 1970) can be greatly reduced in abundance. Thus, the time since the last flood (see Fisher et al. 1982; Fisher 1983, 1987) becomes a critical consideration in community analysis for streams of this type.

Prospectus

Long-term studies and carefully-defined experiments will be necessary to evaluate hypotheses about the broad-scale importance of hydrologic variability on lotic community structure (cf. Callahan 1984). As Schlosser (1987) points out, detecting fish assemblage persistence of shifts in community structure requires multi-year sampling efforts due to between-year variation in environmental conditions and associated ecological processes such as recruitment, age structure, habitat partitioning, and species composition. These same constraints hold for invertebrate assemblages as well.

Conclusion

We believe that the comparative analysis of long-term daily flow records for these 78 widely-distributed streams provides a context in which to evaluate the relative variability of any particular stream's streamflow environment. Given a sufficient record and the statistics that can be derived from it, a stream can be clustered in 11-dimensional flow space (Table 3, Fig. 1) and summarized in four-dimensional (Fig. 3) or arrayed in continuous three-dimensional (Fig. 2) flow space, the axes of which correspond to indices of flow variability having documented ecological significance. The position of a stream in flow space should provide some a priori basis for expectations of relative biotic attributes (both in terms of population and community processes and patterns) that may characterize these streams, all else being equal. However, as all else is never equal on such a broad spatial scale, this streamflow characterization should only be viewed as one conceptual framework that demonstrates the range of streamflow variability and that provides a more objective basis for expectation of ecological attributes (for another see Resh et al. 1988). Although in need of refinement to meet local conditions, our characterization of patterns of temporal hydrographic variation should nevertheless contribute to the development of more quantitative, objective criteria for assessing the relative importance of flow variability and disturbance in structuring stream communities (cf. Wiens 1984). Such criteria are needed for the eventual rigorous linkage of ecological with hydrological data. Also needed, however, is more effort toward assembling long-term biological datasets from streams with reliable long-term flow records.

There is a continuing concern among stream ecologists to relate community pattern and process to environmental variation, including streamflow (Matthews and Heins 1987; Covich 1988; Matthews 1988; Minshall 1988; Power et al. 1988; Resh et al. 1988). Our analysis demonstrates that long-term, daily streamflow records are rich sources of information with which to evaluate temporal and spatial patterns of lotic environmental variability and disturbance across many physiographic and ecographic regions. Only with such a long-term and broad perspective can stream ecologists reliably determine the temporal and spatial scale(s) appropriate in generalizing patterns and processes in lotic communities.

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APPENDIX. Summary data for 78 streams.

State	Map[a] No.	Stream name	USGS Gauge No.	Years in record	AREA (km^2)	ANNQ ($m^3 \cdot s^{-1}$)	Q/AREA ($mm \cdot yr^{-1}$)	LNANNQ ($m^3 \cdot s^{-1}$)	Flood[b] ($m^3 \cdot s^{-1}$)	r^2[c]	PREDQ	C/P	ANNCV	FLODFREQ (yr^{-1})	FLODINT (d)	FLODDUR (d)	FLOD60D (fraction in 60d)	FLODFREE (number of 365 d)	FLODTIME (day of water year)
AL	60	Turkey Creek	02427700	28	253	4.1	435	1.0	98.0	.99	.38	.49	41.7	.75	284	1.5	.61	101	155
AR	57	Cossatot River	07340300	17	232	5.4	742	2.0	132.3	.96	.53	.67	28.9	.71	397	1.4	.50	165	138
	56	Big Piney Creek	07257000	35	710	11.5	502	2.4	256.0	.98	.34	.45	45.9	.71	417	1.2	.52	169	172
	55	Piney Fork	07073500	45	257	2.5	313	0.8	65.7	.98	.33	.55	40.0	1.00	166	1.3	.36	72	162
AZ	26	Aravaipa Creek	09473000	20	1401	1.0	23	0.5	20.2	.94	.27	.98	25.3	.75	189	2.1	.60	190	121
	25	Sycamore Creek	09510200	24	425	0.8	63	0.1	15.9	.98	.30	.47	128.9	1.29	29	2.5	.48	154	122
CA	2	Salsipuedes Creek	11132500	44	122	0.3	77	0.1	7.9	.96	.18	.21	85.7	1.25	37	2.0	.69	210	139
	4	Clark Fork Stanislous River	11292500	35	175	4.5	812	2.3	24.9	.99	.62	.68	22.8	.91	328	11.1	.78	155	235
	5	Sagehen Creek	10343500	32	27	0.4	428	0.2	2.2	.99	.43	.55	40.4	.97	203	10.1	.68	137	216
	6	Big Chico Creek	11384000	56	188	4.2	706	1.8	63.1	.91	.61	.72	23.8	1.25	53	2.0	.59	183	120
	7	Trinity River	11423200	29	386	12.2	999	5.6	104.1	.93	.63	.66	22.4	.83	114	2.1	.50	142	120
	3	Arroyo Seco	11152000	84	633	4.8	244	0.8	93.3	.97	.32	.33	57.5	1.21	51	2.1	.68	222	126
	1	Sespe Creek	11113000	58	650	3.3	159	0.3	80.3	.97	.22	.18	79.8	1.19	57	2.1	.64	223	131
CO	22	East River	09112500	63	749	9.6	401	4.6	58.3	.97	.80	.68	21.3	.70	355	12.5	.98	296	246
	20	Colorado River	09010500	30	138	1.8	414	0.7	13.5	.93	.66	.45	37.5	.77	339	10.9	1.00	331	254
	21	St. Vrain Creek	06724000	81	549	3.7	210	1.4	23.2	.99	.58	.46	35.7	.73	362	8.5	.86	230	254
GA	62	Middle Ocone River	02217500	48	1031	15.0	454	10.3	160.0	.96	.71	.87	12.0	.88	368	1.6	.36	73	288
	61	Satilla River	02226500	48	3108	29.7	294	9.5	213.8	.98	.43	.83	25.1	1.02	176	4.8	.51	58	160
IA	47	Winnebago River	05459500	53	1362	7.5	173	3.1	71.2	.98	.43	.82	23.8	.98	158	2.8	.40	142	233
IL	53	Lusk Creek	03384450	18	111	1.8	516	0.3	58.9	.94	.31	.11	76.2	1.14	116	2.4	.39	109	202
	52	S.Fork Saline River	03382100	20	381	4.8	394	1.1	71.2	.96	.38	.51	43.3	.78	465	1.0	.57	89	181
	51	Vermilion River	05554500	43	1500	11.2	232	2.8	133.6	.96	.35	.59	38.5	1.10	147	2.2	.50	130	180
IN	50	Youngs Creek	03362000	43	277	3.0	341	1.0	68.4	.96	.37	.58	39.4	.70	364	1.1	.37	117	164
KS	39	Rattlesnake Creek	07142300	28	2030	1.0	15	0.5	8.6	.98	.33	.79	26.6	1.07	76	2.8	.40	152	252
	40	Smoky Hill River	06860000	46	9207	0.9	3	0.1	15.7	.98	.16	.31	89.5	1.11	61	3.0	.57	153	271
KY	69	Stoner Creek	03252000	31	619	8.2	418	1.9	187.7	.99	.35	.52	42.9	.71	265	1.1	.46	95	159
	68	Russell Creek	03307000	46	487	8.3	541	2.8	173.3	.96	.44	.68	30.6	.67	395	1.2	.42	65	150
LA	58	Bayou Toro	08025500	29	383	4.1	340	1.0	89.6	.93	.36	.58	38.7	.66	275	1.8	.50	111	128
ME	78	Machias River	01016500	32	855	16.2	596	7.5	161.6	.97	.60	.77	20.6	.59	383	4.1	.84	234	210
MI	49	Augusta Creek	04105700	21	101	1.2	381	1.2	3.3	.70	.76	.92	8.7	.48	336	2.6	.50	176	217
MN	46	Baptism River	04014500	34	363	4.8	416	2.0	58.9	.92	.50	.64	29.9	.82	356	2.3	.61	166	211
MO	54	Cedar Creek	06919500	37	1088	8.7	253	1.3	220.3	.97	.21	.43	56.2	.81	227	1.8	.50	55	19
MS	59	Skuna River	07283000	38	658	10.7	510	1.6	294.4	.96	.35	.57	42.7	.76	232	1.3	.45	187	159
MT	16	Prospect Creek	12390700	29	471	7.3	488	4.0	44.5	.94	.75	.71	19.4	.79	342	4.4	.87	200	227
	17	M. Fork Rock Creek	12332000	48	319	3.5	345	1.9	23.7	.94	.76	.67	22.3	.67	361	8.3	.97	238	242
NC	66	Little Tennessee River	03500000	40	363	11.2	972	9.1	78.7	.98	.76	.89	10.3	.63	373	1.2	.44	109	163
	65	Hunting Creek	02118500	34	401	5.8	458	4.5	79.4	.98	.69	.91	11.0	.74	375	1.1	.36	63	165
	64	Potecasi Creek	02053200	27	583	6.7	361	2.2	53.3	.98	.40	.59	37.5	.85	246	3.5	.30	48	169
ND	45	Mauvis Coulee	05056100	26	1002	0.5	17	0.1	3.4	.90	.52	.69	186.3	.92	318	14.4	.83	216	192
NE	42	Dismal River	06775900	20	2490	5.4	69	5.5	7.2	.60	.79	.96	1.2	.85	191	1.6	.39	127	222
	41	Logan Creek	06799450	22	1890	4.4	74	2.5	95.2	.96	.62	.90	14.8	1.14	179	1.4	.52	197	249
NM	31	Conchas River	07222500	51	1018	0.4	12	0.1	19.2	.96	.35	.79	195.4	.75	285	1.4	.53	207	297
	30	Gallinas River	08380500	61	218	0.5	79	0.3	4.2	.98	.31	.71	36.2	.75	226	7.3	.46	126	285
	27	Gila River	09430500	59	490	2.8	182	2.6	36.1	.97	.63	.88	14.6	1.05	125	3.0	.40	31	141
	29	Pecos River	08378500	57	4828	4.2	27	1.6	13.3	.98	.63	.72	20.6	.77	198	11.0	.80	199	233
	28	Zuni River	09386950	18	2098	0.4	6	0.1	6.9	.88	.36	.40	119.2	.94	320	5.4	.71	143	18
NV	8	Martin Creek	10329500	65	446	1.0	69	0.5	6.4	.99	.23	.99	33.5	1.09	54	5.6	.48	207	165
NY	79	Owego Creek	01514000	48	479	7.9	522	3.3	118.5	.97	.53	.70	27.2	.71	290	1.3	.62	78	169
OH	72	Conneaut Creek	04213000	24	453	7.6	530	3.1	141.9	.96	.50	.66	29.3	.63	368	1.4	.53	90	147
	73	Auglaize River	04186500	45	834	8.1	296	2.5	131.0	.96	.46	.73	30.0	.84	341	1.8	.47	156	162
OK	37	Blue River	07332500	50	1233	7.1	181	2.7	201.5	.97	.44	.85	24.3	.82	245	1.5	.46	79	195
	36	Elm Fork N.F.Red River	07303400	20	1077	1.2	35	0.5	45.0	.87	.41	.68	35.8	1.05	185	1.2	.57	176	246
	38	Dry Creek	07243000	31	179	0.6	104	0.1	32.0	.98	.20	.36	121.2	1.00	176	1.3	.61	61	234
OR	9	S.Fork McKenzie River	14159200	28	414	18.2	1389	14.2	12.7	.95	.82	.83	10.3	.82	325	1.9	.70	250	105
	10	Smith River	14158790	25	42	2.6	1974	1.3	22.5	.89	.52	.55	34.0	.84	334	1.5	.67	221	83
	11	McKenzie River	14158500	41	239	13.4	1769	11.8	37.9	.89	.79	.90	7.1	.68	355	3.8	.61	141	110
	12	Silvies River	10393500	65	2419	5.0	65	1.5	31.1	.93	.46	.51	35.4	.88	307	13.6	.75	214	179
PA	74	Penns Creek	01555000	56	780	12.5	505	7.2	119.7	.97	.63	.81	17.5	.84	247	1.7	.43	61	162
	75	Towanda Creek	01532000	71	554	8.2	469	3.0	152.2	.99	.45	.69	29.7	.72	311	1.2	.49	27	163
SC	63	Upper Three Runs	02197300	18	225	3.0	424	3.0	8.0	.95	.73	.97	4.2	.56	658	1.1	.50	129	119
SD	44	Moreau River	06359500	44	6890	3.8	18	0.6	82.7	.98	.24	.30	68.3	.85	75	4.0	.44	202	202
	43	Keya Paha River	06464500	40	2771	2.0	23	1.2	17.0	.99	.53	.76	22.6	.79	277	4.1	.51	141	187
TN	67	Duck River	03596000	52	277	5.2	596	2.3	127.1	.98	.55	.72	24.5	.60	397	1.2	.55	142	122
TX	33	San Marcos River	08172000	46	2170	10.3	150	6.5	160.0	.96	.65	.96	10.4	.91	181	1.6	.52	65	217
	34	Beaver Creek	08150800	24	557	0.5	27	0.1	30.7	.97	.20	.24	68.3	.75	351	1.1	.50	73	216
	32	Ecleto Creek	08186500	25	619	1.0	53	0.1	50.1	.95	.26	.59	169.2	.80	270	1.8	.50	84	224
	35	North Croton Creek	08082180	21	650	0.4	21	0.1	17.6	.96	.18	.29	111.7	.95	306	1.6	.40	203	272
UT	24	E. Fork Virgin River	09404450	20	179	0.6	107	0.5	2.0	.91	.67	.85	13.0	.75	65	17.7	.69	155	182
	23	Pine Creek	09337000	29	176	0.1	25	0.1	1.4	.93	.25	.45	51.0	.86	350	5.0	.88	225	225
VA	70	Rapidan River	01665000	43	295	4.2	439	2.5	54.9	.97	.53	.80	21.5	.67	333	1.4	.35	53	184
VT	77	Moose River	01134500	37	195	4.1	660	2.2	47.2	.97	.55	.73	24.5	.62	383	2.0	.70	119	201
WA	13	White Salmon River	14121300	21	84	4.3	1620	3.9	14.2	.99	.80	.88	8.2	57	449	5.6	.58	167	95
	14	Newaukum Creek	12108500	32	71	1.7	772	1.3	12.1	.96	.70	.74	18.1	.78	344	2.3	.64	259	105
	15	Green River	12104500	40	249	11.1	1401	6.5	99.0	.97	.66	.74	18.7	.58	379	1.5	.74	256	82
WI	48	Black Earth Creek	05406500	31	118	0.9	243	0.8	7.4	.94	.69	.95	9.6	.74	367	1.2	.57	123	175
WV	71	Williams River	03186500	56	332	9.4	896	4.3	122.1	.99	.48	.76	26.7	.70	401	1.1	.39	43	156
WY	18	S.Fork Shoshone River	06280300	29	769	12.0	494	5.8	92.3	.96	.83	.68	20.8	.59	376	4.1	1.00	332	260
	19	East Fork River	09203000	48	205	2.9	452	0.8	31.3	.95	.52	.48	42.0	.65	366	4.9	1.00	319	250
Mean value				39	931	5.5	408	2.6			.49	.66	41.6	.83	271	3.5	.58	152	
Minimum value				17	27	0.1	3	0.1			.16	.11	1.2	.48	29	1.0	.30	27	
Maximum value				81	9207	29.7	1974	14.2			.83	.99	195.4	1.29	658	17.7	1.00	332	

[a]Refers to Fig. 1.
[b]Represents the estimated bankfull discharge for a 2-yr return interval.
[c]Expresses the conformity of the ranked annual peak flows to a ln-normal distribution used to generate "bankfull discharge" (see text). See text and Table 1 for explanation of other variables.