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Hydrologic disturbance and nutrient effects on benthic community structure in midwestern US streams: a covariance structure analysis

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Abstract. Understanding how lotic communities respond to combinations and gradients of physical disturbance and nutrient inputs is important for the practical management of stream ecosystems, and to add to our knowledge of stream ecology. We used covariance structure analysis to examine the direct and indirect effects of a gradient in nutrient concentration and hydrologic disturbance on benthic community structure in 133 riffles in 97 midwestern US streams. Model results indicated that the relationship between nutrient concentration, algal biomass, and primary consumer biomass was mediated by hydrologic regime. Algal biomass was strongly dependent on nutrient supply in streams where scouring floods reduced primary consumer biomass. In more stable streams, primary consumers depressed algal standing stocks regardless of nutrient concentration. Our results imply that the response of stream benthic communities to nutrient stimulation is highly variable and dependent on physiography and climate because they strongly influence hydrologic disturbance regimes.

Key words: benthic invertebrates, flood, drought, structural equation models, eutrophication, hydraulic stress, stream ecology.

The ways in which disturbance regime, nutrient availability, and herbivory interact to influence trophic structures of lotic systems are complex and poorly understood. Local and regional differences in hydrology, geology, and nutrient availability provide a spatially complex stage for community interactions (Wiley et al. 1997), involving both direct and indirect effects on trophic structure (Wootton et al. 1996, Stevenson 1997). For example, hydrologic disturbance can fundamentally control the distribution and temporal variation of benthic algal (Biggs et al. 1999) and invertebrate communities (Fisher et al. 1982, Grimm and Fisher 1989) in streams and rivers. Such events include both floods (spates) that mobilize and scour organisms from substrata, and droughts that reduce flow velocities and dry portions of channels (Feminella and Resh 1990).

Cessation of stream flow results in loss of aquatic habitat and significant declines of both algal and macroinvertebrate standing stocks (McElravy et al. 1989, Brussock and Brown 1991, Boulton et al. 1992). Drought or low flows can be more predictable than floods (Brussock and Brown 1991), but the extent to which a streambed dries can vary from year to year and among local streams. Because many of the streams examined in our study experienced drought that dried most of or the entire channel, we included both extreme low flows and high flows in assessing effects of hydrologic disturbance on benthic communities. Negative, short-term effects of spate and drought have often been described (Stanford and Ward 1983, Biggs 1996, Feminella 1996), but long-term disturbance regimes are thought to be more important than individual events in shaping community structure (Resh et al. 1988, Poff 1992, Power et al. 1996, Wootton et al. 1996, Townsend et al. 1997). Although comparative studies are rare, it is clear that hydrologic disturbance regimes with relatively frequent high flows cause mortality differentially across trophic levels (Power et al. 1988, Stevenson 1997, Marks et al. 2000). Other lotic ecosystems experience little hydrologic disturbance (Poff and Ward 1989, Wiley et al. 1997) and large-scale mortalities, if they occur at all, have other causes (e.g., Kohler and Wiley 1997).

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Availability of nutrients such as P and N, in particular, can regulate primary production and patterns of biomass accrual in aquatic ecosystems, including streams and rivers (Grimm and Fisher 1989, Stevenson 1997, Biggs 2000). In addition, grazing herbivore populations can regulate algal productivity in many streams (Power et al. 1988, Tuchman and Stevenson 1991, Rosemond 1994, Kohler and Wiley 1997), even in the presence of significant nutrient enrichment (Rosemond et al. 1993).

We examine the effects of hydrologic disturbance and nutrient concentration on variation in benthic algal and macroinvertebrate biomass in wadeable streams. Specifically, we test the hypothesis that hydrologic regime modifies the relationship between nutrients and benthic structure. We hypothesize that both high- and low-flow disturbance can directly influence algal and invertebrate herbivore biomass, but that nutrient concentrations will only indirectly affect invertebrate standing stock via bottom-up trophic transfers. Furthermore, we hypothesize that grazers can exert top-down control of algal standing stock; thus, our model includes reciprocal effects of grazers on algae and algae on grazers. Using covariance structure analysis (Bollen 1989) of data from 133 stream riffles, we develop a model that shows both flood and drought regulate the effects of nutrient concentration and herbivory on benthic biomass in midwestern US streams.

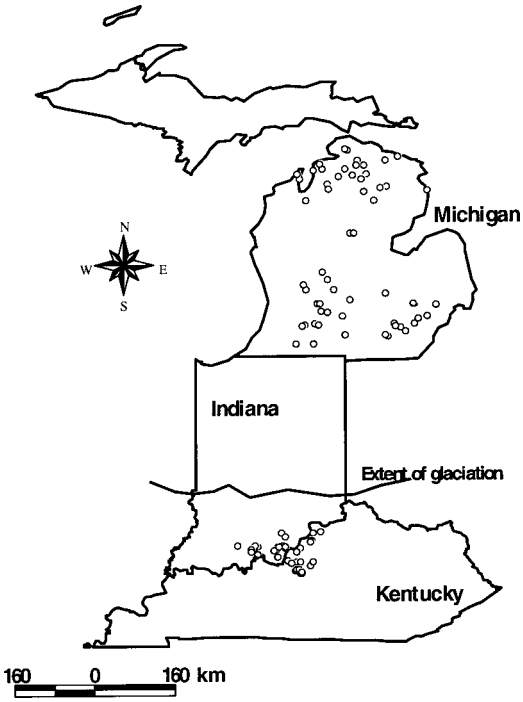

FIG. 1. Location of study sites across Michigan (glacial drift streams), Kentucky, and Indiana (Knobs streams). Stream names, location data, year sampled, and drainage area are given in the Appendix.

Methods

Study sites

Our study evaluated benthic community structure in 133 riffles from 97 stream sites in 2 physiographic regions in the midwestern US during the summers of 1996 and 1997 (Fig. 1). Physiographic regions included the unglaciated Knobs region of northwestern Kentucky and southeastern Indiana (40 sites) and Michigan's glaciated Lower Peninsula (57 sites). Streams in the Knobs region are typified by rapid delivery of precipitation to the stream because of steep topography and underlying limestone bedrock formations (Burroughs 1926, McGrain 1983). Knobs streams typically experience storms of similar magnitude and frequency because large moisture-bearing storms typically travel along a path from the western Gulf region along the Ohio River valley (Burroughs 1926). The glaciated region of Michigan's Lower Peninsula is a large, heterogeneous region of thick soils over sometimes deep glacial drift deposits (Fig. 1). Glacial drift deposits can delay delivery of precipitation to streams resulting in variable inputs of groundwater that contribute to flow stability (Wiley et al. 1997).

Study sites were chosen to represent a range of nutrient levels, land use/land cover types, and hydrologic regimes. Land use/land cover ranged from relatively pristine forested and wetland areas to urban streams. Most stream sites flowed through a mixture of agricultural and forested land. Stream size (Strahler 1952) ranged from 1st to 4th order with 2nd- and 3rd-order streams most common. Most samples were collected from streams in different drainages. However, 8 pairs of sites (4 from each region) were from the same stream in a drainage. In all such cases, the lower site was at least 5 km downstream of the upper site. Of the 133 riffles sampled, 70 samples were collected in

1996 and 63 in 1997, and 36 of the 1997 samples were revisits of sites sampled in 1996.

Interannual independence of flood flows is a common assumption for hydrologic and population time-series analysis in rivers (Gordon et al. 1995, Kohler and Wiley 1997, Cobb et al. 1992). All samples were considered to be statistically independent because there were significant interannual differences in grazer and filter-feeder populations at revisited sites (paired *t*-test, $p < 0.05$) and no interannual correlation for peak discharge and benthic chlorophyll levels (Pearson correlation, $p < 0.05$). To minimize habitat variation among study sites, sampling was conducted in riffle habitats where gravel, cobble, and boulder substrata (typical size ranged from 16 to 256 mm in diameter) predominated. Each riffle was at least 2 m long, with water depths of 10 to 50 cm at the time of sampling.

Measures of channel morphology and hydrologic disturbance

Channel morphology and hydraulic parameters were estimated for each study reach from survey measurements at 3 cross-sections separated equidistantly over reach lengths of 50 to 120 m (Rosgen 1994, Gordon et al. 1995). Bankfull discharge (Q_{bf}) was estimated from the mean bankfull channel area and estimates of flow velocity (ν_{bf}) from the Darcy–Weisbach equation: $\nu_{bf} = 8gR_{bf}S/ff$ where g = gravity constant, R_{bf} = bankfull hydraulic radius, S = slope and ff = resistance coefficient. The resistance coefficient was calculated at bankfull flow depths and the 84% substrate diameter (D_{84}) as follows: $ff = 1/0.82(\log_{10}(4.3(R_{bf}/D_{84})))$ (Knighton 1981, Gordon et al. 1995). D_{84} was used because mobilization of this particle size represents large-scale movement of the streambed (Biggs et al. 1999). The maximum potential for a stream to do work (bankfull power) was calculated as $\Omega_{bf} = (\rho g)Q_{bf}S$, where (ρg) is the specific mass of water, standardized to unit area of the reach. Shear stress equations were used to estimate the diameter of a rock that could be moved at Q_{bf}, $D_{bf} = \tau_{bf}/(\theta_c g(\rho s - \rho w))$ where θ_c is a dimensionless critical shear based on field-estimated streambed packing, ρs and ρw are the density of rocks and water, respectively, and $\tau_{bf} = (\rho g)Q_{bf}S$ (Shields 1936, Knighton 1981). Bed packing differed between regions ($\theta_c = 0.04$ in the Knobs region, $\theta_c = 0.08$ in the glacial drift region). Likewise, in the Knobs region rock density was set at 2.5 kg/m^3 (A. Parola, University of Louisville, personal communication) and in the glacial drift region at 3 kg/m^3 based on measurements of 25 randomly sampled rocks. The Shields shear stress formula approach is typically insufficient to account for intra-riffle variations in bed mobilization at a site and is problematic for localized predictions, as revealed in several small-scale studies (Quinn and Hickey 1990, Death and Winterbourn 1995, Thompson et al. 2002). Other workers have found the Shields equation useful for intersite comparisons of benthic communities (Scrimgeour and Winterbourn 1989, Cobb et al. 1992, Biggs et al. 1999).

This kind of simple force balance approach is appropriate in our regional analysis because of its long history of utility in channel and bank stabilization work, and its correlation with observed variance in benthic insect density (Cobb et al. 1992). The Shields equation does not fully account for differences in streambed armoring and embeddedness, although it does include a term for relative roughness. Bed material in our study streams was well sorted and neither typically embedded nor armored; thus, this issue is a minor concern in our study.

Using the Shields equation, an *index of rock movement at bankfull flow* (BFRM) was calculated as the difference between the diameter of rock (D_{bf}) expected to move at Q_{bf} and the particle size at D_{84}. Negative BFRM values suggest that some portion of the streambed remains stable at Q_{bf}, whereas positive values indicate that most or all of the streambed moves at Q_{bf}. The range in BFRM values was viewed as a gradient in the degree that riffles in a study stream were mobilized during floods.

A *recent substrate movement* index (SMI) was also calculated as BFRM divided by the time (d) from the last-known bankfull event (major flood), using available local USGS gage records ($n = 17$) and field observations. This index was used in our structural model to estimate the relative likelihood that recent bed movements had affected the sampled biological communities (see below).

Estimates of low-flow disturbance were represented by the Q_{90} flow, the discharge that is exceeded 90% of the time, as is common practice (Gordon et al. 1995). The Q_{90} discharge divided

by the bankfull width was used to standardize low-flow events to channel size in different physiographic regions. The bankfull channel was used to standardize low flows because the ecological effect of a low flow depends on its hydraulics (depth, width, velocity) in the channel built by the dominant high flow, typically Q_{bf} (Harvey 1969, Gordon et al. 1995). Flow-duration curves for Knobs streams were obtained from analysis of the frequency of various discharges from USGS gage data ($n = 7$) for several rivers in the Knobs region that were extrapolated to adjacent drainages based on drainage area (Leopold 1994). Q_{90} values for glacial drift streams were based on established flow frequencies for each stream in that region (Seelbach and Wiley 1997).

Summer water temperature was included in our characterization of low-flow disturbance because extreme high temperatures common in Knobs and some urban streams would reduce oxygen concentrations and increase metabolic stress for invertebrates. Mean summer water temperature was measured directly in glacial drift streams. Summer water temperatures for Knobs streams were estimated from USGS water-quality data for Knobs streams ($n = 7$) and regional National Atmospheric and Oceanic Administration (NOAA) air temperature data ($n = 5$). Water temperature in Knobs streams is highly dependent on air temperature and stream size, and was estimated as °C = 7.14 + 0.01(drainage area) + 0.39(summer air temperature) ($R^2 = 0.41$, $F = 147.5$, $p < 0.01$).

Nutrient sampling

Water samples for determining inorganic nutrient concentrations were collected from each study site at 1- (Knobs region, $n = 8$–9) to 2-w (glacial drift region, $n = 4$) intervals during the 2-mo index sampling period (May through June in the Knobs region and July through August in the glaciated region). Index periods were chosen to capture times of maximum algal production and growth following the annual spring high flows (low-water seasons typically begin 2 mo later in Michigan than Kentucky). Algal growth rates and biomass during postflood colonization are hypothesized to better reflect responses to nutrient enrichment than temporally random samples (Stevenson 1996). Water samples were analyzed for NO_x and NH_4 using a Skalar® autoanalyzer (Skalar Inc., Norcross, Georgia, USA), for soluble reactive P (SRP) using a Hitachi® U-2001 spectrophotometer (Hitachi High-Technologies, Tokyo, Japan), and alkalinity according to standard methods (APHA 1998). Conductivity was measured in the field concurrently with water sample collection using a YSI conductivity meter (YSI Inc., Yellow Springs, Ohio, USA). Percent canopy cover was measured at each site using a spherical canopy densiometer to estimate light levels.

Periphyton and invertebrate sampling

Quantitative benthic periphyton and invertebrate samples were collected once from each site during the last 2 wk of the 2-mo sampling period. In the Knobs region, algae and invertebrate samples were collected in all streams within a 4-d period, whereas in the glaciated region sampling occurred over 2 wk because of travel logistics. Floods are far less frequent in the more hydrologically stable drift streams, and algal biomass varied little during the sampling period, so a 2-wk sampling period seemed reasonable.

Benthic algae were sampled from five 3-rock clusters in each riffle. Rocks were scraped, washed, and each 3-rock cluster was combined into 1 sample. Estimates of rock surface areas from which algae were scraped were generated from measures of the upper rock surface made in the field. Chlorophyll *a* was extracted from algal samples with 90% buffered acetone and measured spectrophotometrically (APHA 1998). The 5 samples were then averaged to obtain a measure of chlorophyll *a* per unit area for each site. Invertebrate samples were a composite of rock and Hess samples. Five random clusters of 5 rocks each were collected from the study riffle with a small dip net (250-μm mesh), size), gently brushed, washed, and retained organisms preserved with 70% alcohol. The rock area sampled for invertebrates was determined through image analysis (ImageJ, version 1.32, National Institutes of Health, Bethesda, Maryland). Densities of large-bodied, mobile invertebrates (e.g., *Nigronia* sp., *Acroneuria* sp., *Isonychia* sp.) were estimated from 5 samples collected with a Hess sampler (0.675 m diameter, 1 × 3 mm mesh size). Hess samples were composited for each site and preserved in 70% alcohol. Invertebrate samples were enumerated and identified in the

TABLE 1. Principal Components Analysis of summer water temperature and transposed LnQ_{90}/bankfull width used to create a low-flow disturbance variable for covariance structure analysis (CSA). The 1st principal component (PC) was used in CSA because it accounted for most of the variance of the 2 variables. Mean and SD are for PC1. $n = 133$. Q_{90} = the discharge that is exceeded 90% of the time.

Component	Eigenvalue	% variance explained	Mean	SD	Summer temperature correlation	LnQ_{90}/bankfull/ width correlation
PC1	1.606	80.3	−0.03	0.10	0.73	0.95
PC2	0.394	19.7				

laboratory, and mass of organisms estimated using image analysis and length–mass regressions (Smock 1980, Meyer 1989, Burgherr and Meyer 1997, MJW unpublished data). Taxa were assigned to 1 of 4 functional groups (filter feeder, grazer, shredder, and predator) based on our best estimate of the dominant feeding behavior (Pennak 1989, Merritt and Cummins 1996). Crayfish were excluded from analyses because their relatively large mass masked the effects of changes in other benthic invertebrates.

Data analysis

Our data were analyzed using covariance structure analysis (CSA), a multivariate statistical technique used for assessing direct and indirect interactions in complex systems (Wootton 1994a, Shipley 2000). The CSA model represents a set of explicit linear hypotheses about causal relationships among variables (Bollen 1989, Wootton 1994b, Grace and Pugesek 1997). CSA models are parameterized by fitting the implied system of simultaneous linear equations to the observed variance–covariance matrix using one of several available estimation procedures that minimize the difference between the implied model and sample covariance matrices (Bollen 1989). CSA was useful because it provided a tool for evaluating observed data patterns in a multivariate system where covariance was common and collinearity high (Wootton 1994b, Petraitis et al. 1996, Pugesek and Grace 1998). In contrast to many descriptive multivariate analyses (e.g., multiple linear regression, Canonical Correspondence Analysis), where the goal is to identify statistical dependencies between variables, CSA identifies correspondence between explicit causal assumptions and patterns of correlation and variance in the data set (Bollen 1989). However, CSA cannot be used to prove causation, only to falsify causal hypotheses.

The CSA model can be viewed as a network of hypothesized causal interactions between hydrology, nutrient concentrations, and invertebrate and algal biomass that can then be statistically compared to the structure of the data. Exogenous conceptual variables included high- (Ω_{bf}, SMI) and low-flow disturbance, and nutrient concentrations. Low-flow disturbance was quantified as the combined influence of low flow (Q_{90}/bankfull width) and estimated summer water temperature using Principal Components Analysis (PCA) (Table 1). PCA was used because the individual variables were highly skewed, resulting in violations of multivariate normality and reduction of model fit. PCA minimized this problem. Nutrient concentrations were quantified using mean concentrations of SRP and total inorganic N (NO_x and NH_4). Endogenous variables in the model were algal, grazer, and filter-feeder biomass. However, algal and grazer biomass also were causal variables based on the trophic portion of the model. Detrital pathways were not measured and, thus, were not included in the model.

AMOS 4.0 (Arbuckle and Wothke 1999) was used to fit sample data to the hypothesized model using the maximum likelihood function for model fitting because it is reasonably robust against moderate departures from multivariate normality (Bollen 1989, Grace and Pugesek 1997). Squared multiple correlations were used to determine how well the model explained variability of endogenous variables. Direct, indirect, and total effect coefficients were analyzed for statistical significance (t distribution, $\alpha = 0.05$) using Monte Carlo bootstrapped SEs and for compatibility with theoretical expectations for effects of one variable on another. Standard as-

sumptions of linear modeling such as multivariate normality, independence, linear responses, and additivity were reasonably met (Mitchell 1992). Our sample size of 133, which is relatively large for ecological studies, provided adequate but not excessive power to avoid false acceptance of the test hypothesis (Bollen 1989, Mitchell 1992). The ratio of sample size to estimated paths was 8.3, which is considered large enough to ensure stable parameter estimates (Petraitis et al. 1996).

Simple correlation, multiple linear regression, PCA, and descriptive statistics were performed using SPSS (version 8.0, SPSS Inc., Chicago, Illinois, USA). All variables, except nutrients, were natural log transformed to achieve linearity and approximately normal distributions. Where values of the raw variables were <1, the integer 1 was added to the variable prior to log transformation. Low-flow variables (Q_{90}) were transposed to reflect the potential disturbance effects of extreme low flow. Transformed data were used for all linear models, including covariance structure models.

Results

Interregional variability in streams

Channels in the Knobs region were consistently deeper and narrower ($p < 0.01$) than glacial drift streams (Table 2), and generally lacked features such as undercut banks, tree roots, woody debris, and aquatic macrophytes common to drift streams. Mean hydraulic radius was significantly greater ($p < 0.01$) in Knobs streams (1.10 m) than in glacial drift streams (0.54 m), as were mean Ω_{bf}, τ_{bf}, BFRM, and SMI (Table 2). BFRM values suggested that ~57% of the glacial drift streams could move larger bed particles at Q_{bf}, whereas 100% of the Knobs streams were competent to move most or all of the riffle substrata. The low-flow parameters, Q_{90} and Q_{90}/bankfull width, were significantly lower in the Knobs region ($p < 0.01$). Low flows in the Knobs streams were typically 1 order of magnitude lower than glacial drift streams with primarily runoff inputs, but up to 2 orders of magnitude lower than glacial drift streams dominated by groundwater inputs (Fig. 2A, B).

Although hydrologic and geomorphic attributes differed between glacial drift and Knobs regions, nutrient concentrations did not ($p > 0.09$), reflecting in part our designed attempt to sample similar water-quality gradients in each region (Table 2). Conductivities were not significantly different between regions when corrected for conductivity resulting from to alkalinity ($p > 0.2$). Mean alkalinity values were significantly higher in glacial drift streams than Knobs streams ($p < 0.01$), indicative of groundwater contributions.

Mean benthic algal biomass (benthic chlorophyll *a*) was greater in Knobs streams than glacial drift streams by an order of magnitude (Table 2). In contrast, mean benthic invertebrate biomass was an order of magnitude greater in glacial drift streams than Knobs streams. Likewise, mean biomass of grazers, shredders, filter feeders, and predators (without crayfish) were all significantly greater in glacial drift streams than in Knobs streams ($p < 0.04$).

Structural modeling

We found significant linear relationships between total benthic biomass (ash-free dry mass, AFDM) and both BFRM ($p < 0.01$; Fig. 3A) and SRP ($p = 0.03$; Fig. 3B). When only the most hydrologically unstable streams (lowest Q_{90} and highest BFRM values) were analyzed, the relationship between AFDM and SRP was not significant ($R^2 = 0.04$, $F = 0.1$, $p = 0.77$, $n = 62$). The spatial variation in the strength of the nutrient effect indicated a more complex analysis of causal pathways was required.

The CSA model (Fig. 4) successfully fit the sample covariance matrix (Table 3) based on a variety of standard metrics (Table 4). Our model explained 51% of the observed variance in grazer biomass, 59% of variance in filter-feeder biomass, and 14% of the variance in algal biomass (Fig. 4). The reciprocal relationship between algal and grazer biomass (Fig. 4) had a stability index below 0.3, indicating stable, well-defined reciprocal relationships (Arbuckle and Wothke 1999). Multivariate kurtosis in the data was 2.54, suggesting low to moderate departures from multivariate normality and generally considered acceptable (Bollen 1989).

In the model, algal biomass was strongly and significantly ($p < 0.05$) influenced by the total effects (sum of direct and indirect effects) of 3 variables: high-flow disturbance (0.41), nutrient concentrations (0.32), and grazer biomass (−0.41) (Table 5, Fig. 4). Direct effects are inter-

TABLE 2. Mean and SD for hydrologic, hydraulic, water chemistry, and biological parameters for Knobs and glacial drift streams (n = 133). Q = discharge, Q_{90} = the discharge that is exceeded 90% of the time, Q_{10} = the discharge that is exceeded 10% of the time. Bold indicates significant differences between Knobs and glacial drift regions at $p \leq 0.05$. n = 133.

	Region			
	Knobs		Glacial drift	
Parameter	Mean	SD	Mean	SD
Hydrologic and hydraulic parameters				
Hydraulic radius (m)	**1.10**	0.37	**0.54**	0.32
Slope (m/m)	0.01	0	0.01	0.01
Bankfull depth (m)	**1.19**	0.42	**0.58**	0.33
Bankfull width : depth	**16.53**	7.41	**22.83**	11.39
Rock diameter (D_{84}, m)	**0.12**	0.06	**0.08**	0.03
Rock movement at bankfull Q (BFRM)	**0.09**	0.15	**−0.11**	0.27
Recent substrate movement index (SMI)	**−0.01**	0.07	**−0.07**	0.03
Bankfull power/width (Ω_{bf}, kwatts/m^2)	**0.07**	0.06	**0.01**	0.01
Critical shear stress (N/m^2)	**68.71**	35.17	**129.98**	51.52
Bankfull shear stress (τ_{bf}, N/m^2)	**62.94**	31.51	**21.32**	14.01
Q_{90}/bankfull width (m^3 s^{-1} m^{-1})	**0.00**	0	**0.05**	0.06
Q_{10}/bankfull width (m^3 s^{-1} m^{-1})	**0.04**	0.02	**0.2**	0.16
Water chemistry and temperature				
Soluble reactive P (μg/L)	10.1	7.9	10.5	4.1
Total inorganic N (μg/L)	673	610	591	655
Alkalinity (mg/L)	**106**	48	**188**	44
Conductivity (μS/cm)	**317**	106	**479**	164
Water temperature (°C)	**26**	0.1	**21**	3.6
Benthic biomass				
Algal biomass (chlorophyll *a*) (mg/m^2)	**134.5**	164.4	**43.2**	72.6
Total invertebrate biomass (mg/m^2)	**1836**	2648	**11,855**	15,457
Total invertebrate biomass w/o Decapoda (mg/m^2)	**840**	1014	**9303**	11,292
Invertebrate filter feeder biomass (mg/m^2)	**172**	296	**6430**	9627
Invertebrate grazer biomass (mg/m^2)	**411**	716	**1586**	1673
Invertebrate predator biomass (mg/m^2)	1103	2243	3004	9008
Invertebrate predator biomass w/o Decapoda (mg/m^2)	**107**	113	**452**	878
Invertebrate shredder biomass (mg/m^2)	**151**	379	**835**	1957

preted like standardized regression coefficients and indicate the magnitude of the unmediated effect of one variable on another, whereas indirect effects are the effects between 2 variables mediated by an intervening variable (Shipley 2000). High-flow disturbance (Ω_{bf}, SMI) had a strong positive, but indirect effect, on algal standing stock (0.36), suggesting a negative effect of floods on grazers, the mediating variable. Nutrients had a strong positive direct effect on algae, although the effect was reduced somewhat by indirect effects of nutrients on grazers. The negative direct effect of grazers on algae (−0.52) was strong, with weak positive indirect effects (0.12).

High-flow disturbance and algal biomass strongly and significantly influenced grazer biomass (total effects of −0.69 and 0.43, respectively). The direct effect of high-flow disturbance on grazer biomass was strongly negative (−0.92), although the total effect was reduced somewhat by positive indirect effects (0.23) mediated through the trophic feedback loop (Fig. 4). In the trophic feedback loop, negative effects of high-flow disturbance on grazers had a positive effect on algal biomass, which in turn had a positive effect on grazer biomass. Nutrients had a positive indirect effect (0.22) on grazer biomass. Although not significant, grazers had a negative indirect effect

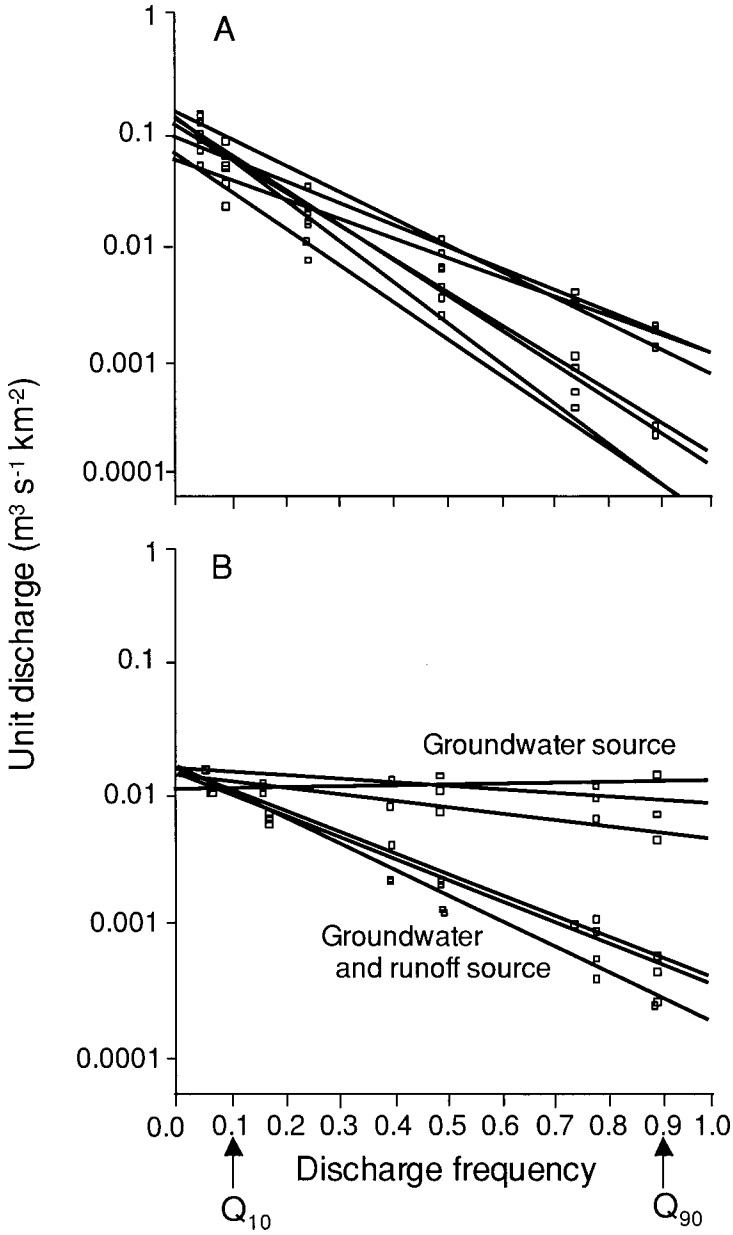

FIG. 2. Hydrographs from 13 available long-term (6–30 y) US Geological Survey gage records, plotting flow exceedance versus discharge standardized by drainage area ($m^3\ s^{-1}\ km^{-2}$). Representative flow-duration curves reflect the magnitude of difference between high- and low-flow yields for Knobs (A) and glacial drift (B) streams, and variability as a result of water source. Q_{10} and Q_{90} as in Table 2.

(−0.22) on themselves. Low-flow disturbance had only small and statistically insignificant effects on grazers. Filter-feeder biomass was strongly influenced by the total effects of high- and low-flow disturbance (−0.36 and −0.41, respectively) and algal biomass (0.29) as a result of strong, significant direct effects. Nutrients had moderate, positive (0.15) and grazers moderate, negative (−0.15) indirect effects on filter-feeder biomass.

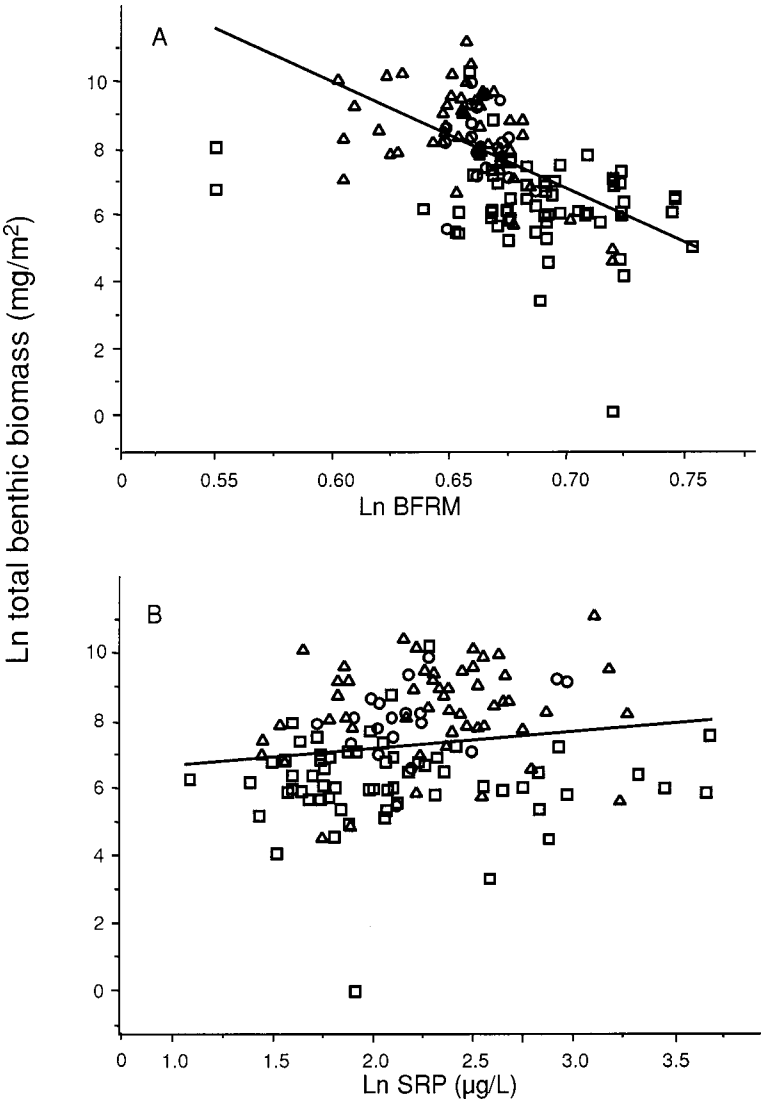

FIG. 3. Relationship between Ln total benthic biomass (ash-free dry mass) and the index of rock movement at bankfull discharge (BFRM) ($R^2 = 0.46$, $F = 111.17$, $p < 0.0005$) (A) and Ln soluble reactive P (SRP) ($R^2 = 0.04$, $F = 4.75$, $p = 0.03$) (B). Sites are classified hydrologically based on the lowest discharge that is exceeded 90% of the time (Q_{90}) and highest BFRM values into 3 categories for the sake of visual comparison: □ = hydrologically variable runoff-fed streams with minimal summer base flows, Δ = hydrologically mixed-source streams with moderate base flows, o = hydrologically constant groundwater-fed streams with high summer base flows. $n = 133$.

Discussion

The CSA model suggested hydrology and nutrient concentration interact to shape broad patterns of biotic composition and energy flow through benthic food webs in small- to medium-sized streams of the midwestern US. This general result is consistent with many earlier field studies indicating a strong influence of individual hydrologic events and long-term hydrologic regimes (Biggs and Close 1989, Grimm and Fisher 1989, Death and Winterbourn 1995). For example, Biggs (1996) found that benthic algal community structure in New Zealand

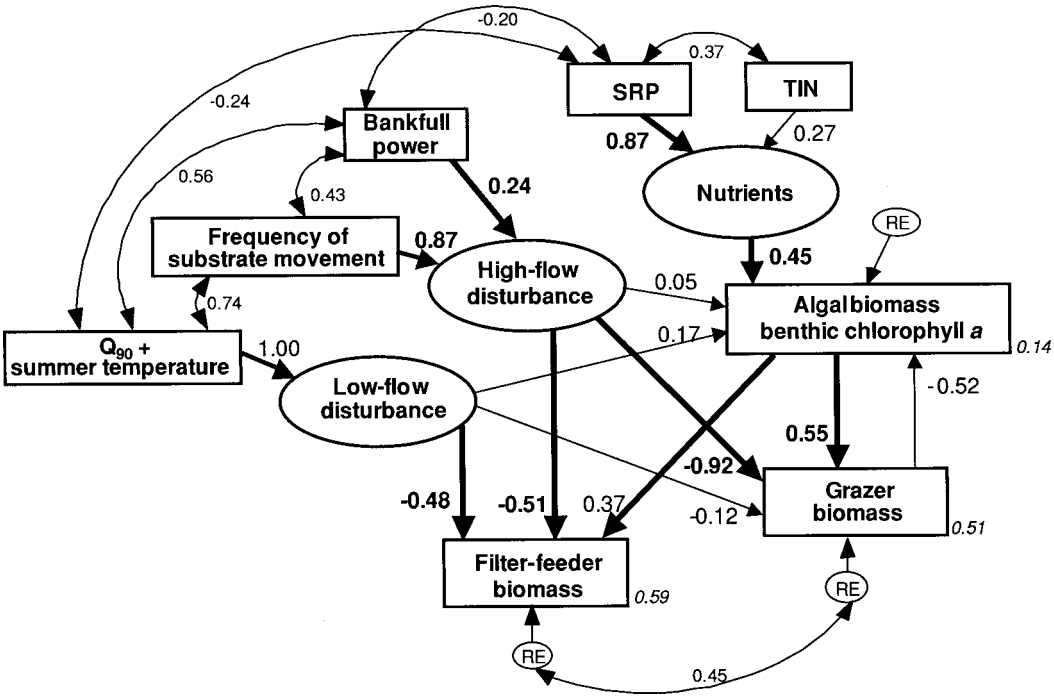

FIG. 4. Fitted path diagram illustrating results of covariance structure analysis (CSA) of the effects of hydrologic disturbance on benthic algal and primary consumer biomass in Knobs and glacial drift streams. Rectangles are measured variables, ovals are unmeasured conceptual variables, and small ovals are residual errors (RE). Arrows indicate direct effects and adjacent numbers are the magnitude of direct effects; bold numbers and thick arrows indicate significant effects at $p < 0.05$. Numbers in italics are squared multiple correlations. $n = 133$. SRP = soluble reactive P, TIN = total inorganic N.

streams varied depending on flood-flow frequency and severity. Likewise, a 3-y study of mountain streams in New Mexico found that interannual differences in algal and grazer densities and stream community function were influenced by annual variations in snowmelt conditions (Peterson et al. 2001).

Disturbance affects community response to nutrients

Our results suggest that high-flow disturbance reduced both grazer and filter-feeder biomass and, through the reduction of grazers, had strong positive indirect effects on algal standing stock. In streams with high disturbance regimes, algae were able to respond to increasing levels of nutrients. However, in streams with low disturbance regimes, herbivore biomass was sufficient to regulate algal populations and nutrient effects were manifested through increased insect biomass rather than increased algal biomass. These results are consistent with predictions by Power et al. (1996) that, in streams with frequent scouring floods, top-down control of algae by grazers is disrupted and trophic transfer of nutrients to upper levels of the food web is reduced. Likewise, in a study of New Zealand rivers, the flood regime was at least as important as nutrients for periphyton accrual (Biggs and Close 1989). In another study of New Zealand rivers, Biggs et al. (1999) suggested that increasing frequency of bed-moving events may effect a shift from top-down to bottom-up control of periphyton. In many hydraulically stable groundwater streams in the glacial drift region, benthic algal biomass varied temporally with primary consumer density (Wiley et al. 1997). Consistent with our analysis, algal biomass increased by an order of magnitude when the biomass of the dominant grazer was reduced by disease (Kohler and Wiley 1992, 1997). In this case, disease and hydraulic disturbance played parallel roles, regulating the top-down control of algal populations. Similarly, the

TABLE 3. Variance/covariance sample matrix for computing covariance structure analysis (CSA). n = 133. Q_{90} = the discharge that is exceeded 90% of the time, SRP = soluble reactive P, TIN = total inorganic N.

	Frequency of substrate movements	Bankfull power	Q_{90} and summer temperature	TIN	SRP	Benthic algal biomass	Grazer biomass	Filter-feeder biomass
Frequency of substrate movement	0.133							
Bankfull power	0.007	0.002						
Q_{90} and summer temperature	0.267	0.025	0.987					
TIN	0.064	0.004	0.095	1.245				
SRP	0.023	−0.003	−0.076	0.211	0.242			
Benthic algal biomass	−0.323	−0.033	−0.787	−0.037	0.097	2.009		
Grazer biomass	0.300	0.015	0.622	0.464	0.219	−0.399	1.813	
Filter-feeder biomass	−0.590	−0.049	−1.752	−0.036	0.213	−0.706	2.434	6.190

increased density of a dominant caddisfly grazer had a strong negative effect on algal biomass in a California stream with stable flow (Feminella and Resh 1990).

Differential flood and drought effects on consumer guilds

Our CSA model suggested that both floods and droughts have important, although different, effects on various functional components of the benthic community. High flows that move riffle substrata had moderate (negative) effects on filter-feeder biomass but strong negative effects (2× greater) on grazer biomass. In contrast, low flows had strong negative effects on filter-feeder biomass, >4× as strong as the effects on grazer biomass. Filter-feeder biomass was ~20% of the total benthic biomass (without crayfish) in Knobs streams and 70% in drift streams. There may be several reasons for this difference. Many filter feeders have, as a part of their feeding strategies, anchoring and attachment adaptations that allow them to maintain position in high-velocity environments and may, therefore, be more resistant to flood flows than grazers (Reice et al. 1990). Filter feeders rely on supplies of fine seston and, thus, are dependent on the competency of flowing water to deliver food particles. As a

TABLE 4. Several standard indices of approximate fit that quantify how well our covariance structure analysis (CSA) model fit the observed data set (Bollen 1989, Mitchell 1992, Browne and Cudeck 1993, Shipley 2000). n = 133.

Model fit index	Test statistic	Rule for good fit	Definition
Chi-square (χ^2)	χ^2 = 12.07, df = 9, p = 0.21	$p > 0.05$	Tests hypothesis that absolute difference between data and the model is not significant
Root mean square error of approximation (RMSEA)	0.05	RMSEA ≤ 0.05	Tests hypothesis that difference between observed and modeled covariances are 0
Tucker–Lewis Index (TLI)	0.98	TLI > 0.9	Comparative evaluation index especially robust to sample size
Normed fit index (NFI)	0.99	NFI > 0.9	Comparative evaluation index similar to TLI but scaled from 0 to 1.0

TABLE 5. Standardized direct, indirect, and total effects for the fitted model. Direct effects are interpreted like standardized regression coefficients (effect of one variable on another with all other variables held constant) and indirect effects are the effects between 2 variables mediated by intervening variables. Total effects are the sum of direct and indirect effects. Bold indicates significance at $p \leq 0.05$. $n = 133$.

	Effects		
	Direct	Indirect	Total
Algae			
Low-flow disturbance	0.17	0.01	0.18
High-flow disturbance	0.05	**0.36**	**0.41**
Nutrients	**0.45**	−0.13	**0.32**
Algal biomass	0	−0.22	−0.22
Grazer biomass	**−0.52**	0.12	**−0.41**
Grazers			
Low-flow disturbance	−0.12	0.10	0.02
High-flow disturbance	**−0.92**	0.23	**−0.69**
Nutrients	0	**0.22**	**0.22**
Algal biomass	**0.55**	−0.12	**0.43**
Grazer biomass	0	−0.22	−0.22
Filter-Feeders			
Low-flow disturbance	**−0.48**	0.07	**−0.41**
High-flow disturbance	**−0.51**	**0.15**	**−0.36**
Nutrients	0	**0.15**	**0.15**
Algal biomass	**0.37**	−0.08	**0.29**
Grazer biomass	0	−0.15	−0.15

consequence, filter feeders have been frequently observed to colonize high-velocity areas and are typically absent in pools and slow-velocity patches (Brussock and Brown 1991, Mackay 1992). Reduced filter-feeder abundances in response to low summer stream flow has been observed in other studies (McElravy et al. 1989, Brussock and Brown 1991, Miller and Golladay 1996). At low flow, the slow velocity in runs and pools can support scraping and gathering invertebrates if the oxygen concentration is adequate and temperatures are not extreme. Although both grazers and filter feeders would be expected to experience the detrimental effects of desiccation, higher temperatures, and reduced oxygen concentrations typical of drought, low flows likely affect filter feeders more severely by reducing or eliminating the transport of food particles.

Our data also suggest that low-flow disturbance was a factor influencing the assemblage of the filtering community in these stream riffles. The Hydropsychidae is a common, large-bodied, filtering caddisfly in many streams worldwide (Wiggins 1996). They have long life cycles and construct energetically demanding woven silk net retreats to capture food particles. Both long life cycles and fixed retreats are supported by permanent stream flow (Brussock and Brown 1991). Hydropsychid caddisflies composed 75% of the filter-feeder biomass in glacial drift streams, but 16% in Knobs streams. The primary component of filter-feeder biomass in Knobs streams was the blackfly *Simulium* sp. (60%), which has a relatively short life cycle, egg diapause, and good dispersal adaptations, allowing greater survival of the predictable but intense low flows typical of Knobs streams (Miller and Golladay 1996).

Regional variation and the influence of disturbance regime

We found that a causal model addressing interactions between nutrient supply, disturbance regime, and benthic biota was statistically consistent with observed variations in riffle community structure across a hydrologically and geologically diverse sample of midwestern streams. Biggs et al. (1999) suggested that disturbance intensity, measured as substrate mobility, may be an important factor generating large-scale patterns in benthic communities. Because hydrogeomorphic regime is linked to landscape context and pattern (geology, topography, and climate), our model indicates benthic communities can be expected to be structurally distinct wherever regional hydrogeology leads to differences in disturbance regime. An insight from our results is not that there are regional differences between communities, but that an understanding of the processes that interact to produce those differences can help explain patterns of spatial variability in stream benthic community structure.

In general, our model predicts that severe hydrologic regimes reduce total benthic biomass by several orders of magnitude compared to less-disturbed streams at mean nutrient concentrations in our study (Table 6). In streams where both high- and low-flow disturbance is severe, our model predicted that absolute and relative biomass of grazers was reduced and algal biomass increased by an order of magnitude, a response to reduced grazing pressure. Commu-

TABLE 6. Mean biomass (mg/m^2) and % (in parentheses) of total benthic biomass for algae (as chlorophyll *a*), grazers, and filter feeders predicted from covariance structure analysis (CSA) coefficients for a range of hydrologic disturbance regimes and mean nutrient concentrations of streams. Low- and high-flow disturbance increase from low to moderate to high (−3, 0, and +3 SDs from the mean disturbance variables in our study). $n = 33$.

	High-flow disturbance					
	Low		Moderate		High	
Low-flow disturbance						
High						
Algae	12.05	(0.2)	77.27	(14.3)	495.70	(94.3)
Grazers	6876.00	(96.8)	444.96	(82.7)	28.79	(5.5)
Filter feeders	211.75	(3.0)	16.02	(3.0)	1.21	(0.2)
Total	7099.80	(100.0)	538.25	(100.0)	525.71	(100.0)
Moderate						
Algae	5.57	(0.0)	35.73	(4.1)	229.19	(80.0)
Grazers	7420.00	(61.6)	480.15	(55.5)	31.07	(10.8)
Filter feeders	4616.00	(38.4)	349.25	(40.4)	26.43	(9.2)
Total	12,041.57	(100.0)	865.13	(100.0)	286.69	(100.0)
Low						
Algae	2.58	(0.0)	16.52	(0.2)	105.97	(14.8)
Grazers	8007.00	(44.3)	518.13	(6.4)	33.53	(4.7)
Filter feeders	10,060.00	(55.7)	7613.00	(93.4)	576.05	(80.5)
Total	18,069.58	(100.0)	8147.65	(100.0)	715.54	(100.0)

nity response to nutrient increases varied depending on both the total extent of hydrologic disturbance and relative importance of high and low flows (Fig. 5). If low-flow disturbance is greater than high-flow disturbance, the model predicts that grazers will dominate and their biomass will positively respond to nutrient increases, but little response to nutrients will be seen in algal biomass (Fig. 5A, B). If low-flow disturbance is small, the model suggests that filter feeders dominate the benthic community and filter-feeder biomass will strongly respond to nutrient increases (Fig. 5C, F, I). When both types of flow disturbance are moderate to severe, grazers and filter feeders are rare, algal biomass dominates, and algal biomass is sensitive to increased nutrients (Fig. 5D, G, H).

Observations from systems with contrasting hydrologic regimes could be used to test these model predictions. For example, our analysis suggests that groundwater-influenced glacial drift streams should be represented by panels B and E in Fig. 5, in which invertebrate primary consumers respond to nutrient gradients but algae do not. In contrast, Knobs streams are represented by panels D and G in Fig. 5, in which algae primarily respond to nutrient inputs and invertebrate biomass is low, irrespective of nutrient level. In mountain streams in Maine (MJW and S. L. Kohler, Western Michigan University, unpublished data), where low-flow disturbance is low to moderate but high-flow disturbance is relatively severe and common, benthic invertebrate biomass is intermediate and is dominated by either filter feeders or grazers (Table 6, Fig. 5E, F). In New Zealand streams with frequent, extreme scour and drought events (Biggs et al. 1999), all benthic invertebrate biomass is reduced (Table 6, Fig. 5D, G, H cf. Fig. 5B, C, F). Although other factors, including invertebrate life-cycle adaptations to disturbance and recolonization rates for algae and invertebrates following disturbances (Scrimgeour and Winterbourn 1989), can influence benthic community structure, a more thorough understanding of how hydrologic regime can shape stream benthic communities is essential to unraveling the role of nutrient enrichment in lotic ecosystems.

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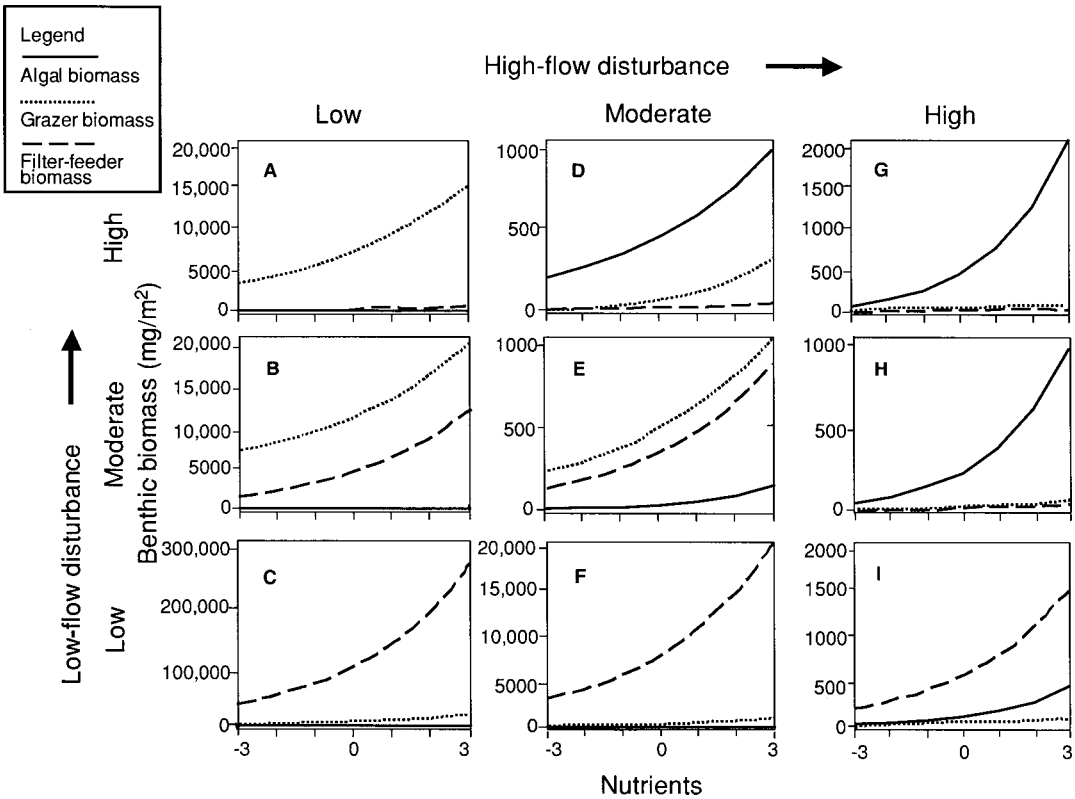

FIG. 5. Relative effects of nutrients and hydrologic disturbance on algal, grazer, and filter-feeder biomass in Knobs and glacial drift streams. Graphs are solutions of iterative, simultaneous equations taken from the parameterized covariance model and, thus, are predictive equations. Low-flow disturbance increases (−3 to +3 SDs from the mean) from bottom to top and high-flow disturbance increases (−3 to +3 SDs from the mean) from left to right in the series of plots. Nutrients increase (−3 to +3 SDs from mean) from left to right in each plot. Note different scales for benthic biomass in each plot. $n = 133$.

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APPENDIX. Stream name, site location, sample year and drainage area, where IN = Indiana, KY = Kentucky, and MI = Michigan. n = 133.

Stream	State	Coordinates		Year sampled		Drainage area (km^2)
		Latitude	Longitude	1996	1997	
Bird Hollow	IN	38.359	−86.767	*	*	6.6
Bogard Creek	IN	38.294	−86.432	*	*	33.7
Brownstown Creek	IN	38.347	−86.480	*	*	14.0
Brushy Creek	IN	38.305	−86.438	*	*	11.5
Buck Creek	IN	38.143	−86.044	*	*	42.1
Camp Fork Creek	IN	38.343	−86.411	*	*	7.0
Corn Creek	IN	38.325	−86.040	*	*	41.1
Crandall Branch	IN	38.286	−86.066	*	*	11.0
Dog Creek	IN	38.358	−86.453	*	*	11.2
Jersey Park Creek	IN	38.370	−85.964	*	*	25.1
Little Indian Creek	IN	38.309	−85.906	*	*	33.1
Middle Fork Blue River	IN	38.589	−85.975		*	54.0
Middle Fork Buck Creek	IN	38.142	−86.042	*	*	34.2
Middle Fork Indian Creek	IN	38.361	−85.958	*	*	60.2
Otter Creek	IN	38.297	−86.525	*	*	33.1
Raccoon Branch	IN	38.275	−86.097	*	*	15.7
Richland Creek	IN	38.324	−86.012	*	*	22.5
South Fork Blue River	IN	38.526	−85.917		*	39.1
Stinking Fork	IN	38.233	−86.529	*	*	21.3
Turkey Fork	IN	38.203	−86.405	*	*	41.5
Whiskey Run	IN	38.518	−85.917		*	19.5
Yellow Fork	IN	38.346	−85.913	*	*	5.5
Barebone Creek	KY	38.586	−85.400		*	23.3
Bluelick Creek	KY	38.027	−85.694	*		20.1
Cain Run	KY	38.068	−85.867	*		9.8
Cedar Creek	KY	38.418	−85.449	*	*	32.6
Crooked Creek	KY	37.890	−85.720	*	*	17.0
Goose Creek	KY	38.303	−85.625	*	*	22.4
Hardy Creek	KY	38.607	−85.269		*	25.1
Harrison Fork	KY	37.867	−85.601		*	9.8
Harts Run	KY	37.864	−85.615	*	*	8.0
Knob Creek	KY	38.044	−85.794	*	*	12.9
Lickskillet Creek	KY	37.934	−85.653	*	*	12.0
Long Lick Creek	KY	37.932	−85.705	*	*	41.4
Lower Wilson Creek	KY	37.867	−85.614	*	*	33.0
Middle Branch Harrods Creek	KY	38.449	−85.418		*	58.6
Middle Fork Beargrass Creek	KY	38.241	−85.700	*	*	52.7
Overalls Creek	KY	37.873	−85.602	*	*	8.6
Pryors Fork	KY	38.058	−85.410		*	21.5
Upper Wilson Creek	KY	37.873	−85.601		*	14.2
Antrim Creek	MI	45.174	−85.371	*		4.0
Augusta Creek	MI	42.388	−85.353	*	*	75.0
Battle Creek	MI	42.539	−84.849	*	*	432.0
Belangers Creek	MI	45.018	−85.617	*		28.0
Big Creek	MI	44.627	−84.271	*		201.0
Black River–Crooked Rapids	MI	44.815	−83.302	*		174.1
Black River–Tin Shanty	MI	45.126	−84.411	*		106.0
Boardman River	MI	44.637	−85.517	*		82.0
Cedar River	MI	44.942	−85.119	*		22.0
Coldwater River	MI	42.769	−85.310		*	209.0
Cranberry Creek	MI	44.046	−84.706	*		18.1
Dickerson Creek	MI	43.186	−85.134		*	97.0

APPENDIX. Continued.

Stream	State	Coordinates		Year sampled		Drainage area (km^2)
		Latitude	Longitude	1996	1997	
East Branch Maple River	MI	45.548	−84.754	*	*	162.0
Egypt Creek	MI	43.015	−85.511		*	16.6
Flat River	MI	43.329	−85.209		*	365.0
Franklin Creek	MI	42.532	−83.306		*	38.0
Gilchrest Creek	MI	44.879	−84.066	*		47.0
Honey Creek	MI	42.317	−83.797	*		59.9
Hunt Creek	MI	44.854	−84.157	*	*	13.0
Huron River	MI	42.386	−83.912	*		1143.4
Irontone	MI	45.078	−84.675	*		7.0
Johnson Drain	MI	42.382	−83.547		*	32.0
Jordan river	MI	45.064	−84.925	*		3.3
Little Sturgeon river	MI	45.365	−84.578	*	*	29.1
Looking Glass River	MI	42.818	−84.721		*	690.0
Malletts Creek	MI	42.253	−83.699	*		12.8
Middle Branch Rouge River	MI	42.476	−83.477		*	24.0
Messer Brook	MI	42.761	−85.257		*	30.0
Mill Creek	MI	42.339	−83.891	*		373.5
Monroe Creek	MI	45.209	−85.207	*		11.0
Nottawa Creek	MI	42.013	−85.380		*	459.0
Ocqueoc river	MI	45.365	−84.079		*	143.0
Paint Creek	MI	42.727	−83.158		*	162.0
Pigeon River	MI	45.273	−84.461	*		233.0
Prairie Creek	MI	43.011	−85.017		*	244.0
Raisin River–Austin Rd	MI	42.146	−84.014	*		378.0
Raisin River–Sharon Valley Rd	MI	42.168	−84.076	*		329.0
Rapid River	MI	44.824	−85.099	*		23.0
Roaring Brook	MI	45.098	−85.670	*		5.0
Rocky River	MI	42.024	−85.719		*	175.0
Rogue River	MI	43.109	−85.567		*	649.0
South Branch Kalamazoo River	MI	42.194	−84.788	*		385.0
South Branch Pigeon River	MI	45.030	−84.514	*		24.0
Seven Mile Creek	MI	42.378	−85.290	*	*	36.0
Shiawassee River–Bancroft Rd	MI	42.936	−84.071	*		1059.0
Shiawassee River–Eagle Rd	MI	42.769	−83.576	*		37.0
Shiawassee River–Eaton Rd	MI	42.754	−83.539	*		22.0
Silver Creek	MI	42.330	−85.586	*		17.0
Spring Brook–Kalamazoo drainage	MI	42.364	−85.529	*	*	88.0
Spring Brook–Bear River drainage	MI	45.206	−84.808	*		2.0
Stover Creek	MI	45.299	−85.257	*		15.0
Thornapple River–Airport	MI	42.625	−85.245		*	1084.0
Thornapple River–River Rd	MI	42.611	−85.126		*	661.0
Trout River	MI	45.429	−83.843		*	94.0
West Branch Cedar River	MI	44.033	−84.647	*		83.0
West Branch Maple River	MI	45.564	−84.806	*	*	215.0
West Branch Sturgeon River	MI	45.276	−84.602	*		459.0