Effective discharge analysis of ecological processes in streams

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[1] Discharge is a master variable that controls many processes in stream ecosystems. However, there is uncertainty of which discharges are most important for driving particular ecological processes and thus how flow regime may influence entire stream ecosystems. Here the analytical method of effective discharge from fluvial geomorphology is used to analyze the interaction between frequency and magnitude of discharge events that drive organic matter transport, algal growth, nutrient retention, macroinvertebrate disturbance, and habitat availability. We quantify the ecological effective discharge using a synthesis of previously published studies and modeling from a range of study sites. An analytical expression is then developed for a particular case of ecological effective discharge and is used to explore how effective discharge varies within variable hydrologic regimes. Our results suggest that a range of discharges is important for different ecological processes in an individual stream. Discharges are not equally important; instead, effective discharge values exist that correspond to near modal flows and moderate floods for the variable sets examined. We suggest four types of ecological response to discharge variability: discharge as a transport mechanism, regulator of habitat, process modulator, and disturbance. Effective discharge analysis will perform well when there is a unique, essentially instantaneous relationship between discharge and an ecological process and poorly when effects of discharge are delayed or confounded by legacy effects. Despite some limitations the conceptual and analytical utility of the effective discharge analysis allows exploring general questions about how hydrologic variability influences various ecological processes in streams.

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1. Introduction

1.1. Discharge Analysis in River Sciences

[2] One of the most influential paradigms of fluvial geomorphology is that of effective discharge. *Wolman and Miller*'s [1960] suggestion that frequency of geomorphic process matters as much as magnitude of process led to the view that most fluvial landforms are shaped by frequently occurring moderate floods, rather than by rare, cataclysmic floods. Today, calculation of effective discharge is a foundational analysis of channel change and the estimation of in-stream flows, as well as in the burgeoning industry of river restoration channel design.

[3] Over the past decade, ecologists have shown the significance of flow regime in stream ecosystems. Discharge has been suggested to be a "master variable" that limits the distribution and abundance of species [*Power et al.*, 1995] and regulates the ecological integrity of flowing water systems [*Poff et al.*, 1997]. Yet despite the recognition of the importance of discharge to both stream ecology and fluvial geomorphology, there is surprisingly little similarity in how the two disciplines have treated the effects of flow regime. Whereas geomorphologists have emphasized developing explicit and quantitative relationships between discharge and geomorphic variables, links between ecological variables and discharge tend to be less direct. Such lack of similarity in approaches appears to be a key limitation in linking the fields of geomorphology and ecology [*Benda et al.*, 2002]. The ubiquitous application of effective discharge in fluvial geomorphology, and the need for a common approach to analyzing the influence of discharge on stream ecosystems, suggests that the effective discharge concept may have relevance to allied disciplines that also study the natural science of the river, particularly stream ecology.

1.2. Magnitude, Frequency, and Effective Discharge in Geomorphology

[4] While many interrelated variables affect stream form, discharge is the primary influence on sediment transport and channel morphology in alluvial streams, and geomorphologists have focused considerable effort on identifying how discharge drives changes in channel form. Quantitatively linking discharge to geomorphic processes led to the development of one of the most influential paradigms of fluvial

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geomorphology: effective discharge. Given near steady state conditions over moderate timescales, a discharge range can be found which transports the most sediment given its frequency of occurrence. *Wolman and Miller* [1960] called this discharge the "effective discharge" because it accomplished the most geomorphic work compared to other flows. Large discharges might individually transport much more sediment than smaller discharges, but are so rare that they do not have the same opportunity for sediment transport as their smaller counterparts. Thus Wolman and Miller suggested that there is a balance between the frequency and magnitude of events, such that some moderate discharge, likely neither the largest nor the most frequent, would be geomorphologically most effective over time.

[5] For actual calculation, the long-term geomorphic effectiveness of a flood of a particular magnitude is the product of the effect of that flow multiplied by its frequency of occurrence. A flow duration curve can be created using historic discharge records (Figure 1), represented by $f(Q)$ hereafter. The geomorphic effect of a given flood is determined from the sediment discharge rating curve (sediment load vs. discharge over the entire range of discharges experienced by the channel, curve $S(Q)$ in Figure 1). The product of the hydrologic frequency curve and the sediment rating curve is the effectiveness curve, which represents the proportion of the total annual sediment load carried by each increment of discharge ($E(Q)$ in Figure 1). The modal value of $E(Q)$ is then the effective discharge. Thus the effective discharge depends on the statistical representation of stream flows, the shape of the sediment rating curve, and the threshold at which transport begins [*Baker*, 1977; *Andrews*, 1980]. Because sediment rating curves are often strongly nonlinear [*Emmett and Wolman*, 2002], moderate floods (i.e., those with recurrence intervals of 1 to 5 years) tend to be most effective for sediment transport through time. This relationship is consistent over an extremely large range of drainage areas, channel types, and climatic regimes [*Nash*, 1994], although there are exceptions (discussed below).

[6] What intrigues most geomorphologists is the correspondence between the calculated effective discharge and the field condition of bank-full stage and bank-full discharge. Research subsequent to Wolman and Miller's introduction of the effective discharge concept has often shown that in alluvial channels at equilibrium with constraining conditions, channel bank-full geometry is adjusted such that bank-full discharge is similar to the effective discharge [*Andrews*, 1980; *Emmett and Wolman*, 2002]. That is, channels appear to adjust their geometry to allow the greatest sediment conveyance over time, although the mechanisms for this remain unknown. Nevertheless, sediment transport is the primary geomorphic work done by discharge in a river system, and there is obvious correspondence between the distribution of work associated with sediment transport and the work of maintaining channel form.

[7] Although substantial attention is given to the discharge corresponding to the mode of the effectiveness curve and to bank-full discharge, i.e., the actual value of the effective discharge, one can take a broader view of the utility of effective discharge analysis in that it quantitatively identifies the range of discharges within which most sediment transport occurs. That is, more generally, given a discharge-dependant function of a process, effective discharge analysis is a tool with which to evaluate the range of discharges (e.g., baseflow or rare flood) most important for the process of interest.

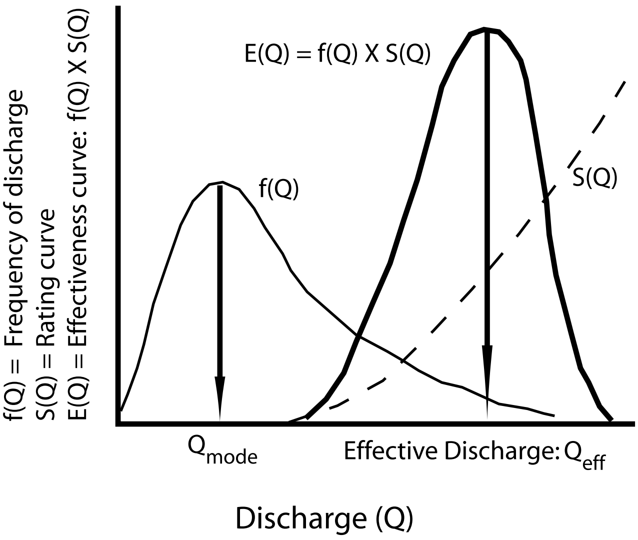

Figure 1. Components of effective discharge (Q_{eff}). Adapted from *Wolman and Miller* [1960].

1.3. Applying Effective Discharge to Stream Ecology

[8] Many ecological processes are known to be discharge-dependent, such as the flux of nutrients and organic material, while others have the potential to be discharge-dependent, such as macroinvertebrate drift. The utility of effective discharge analysis in geomorphologic analysis of fluvial landforms suggests that it may be usable in aquatic ecology as well. *Doyle* [2005] applied an effectiveness analysis to nutrient retention in streams using a theoretical modeling approach and showed that the most effective discharges for nutrient retention are those at and below the modal discharge. More generally, his analysis suggested that effective discharge analysis was a useful tool for examining processes other than sediment transport, particularly some ecological processes.

[9] Here we explore the interaction of magnitude and frequency in ecological processes by applying effective discharge analysis (hereafter Q_{eff} refers to ecological effective discharge), to stream ecosystems. The goal of this paper is to explore what insight into ecological processes can be gained by using the effective discharge analysis, and more specifically, to what extent the concept is applicable to an array of ecological variables. We suggest effective discharge as an objective framework for examining the strength and nature of the relationship between discharge and ecological response, and how these relationships vary among different ecological variables or among different streams. We draw from a wide range of ecological variables using data derived from previously published studies. In cases where data were not available, modeling approaches are used. In addition, a simple modeling approach is developed to analyze Q_{eff} for ecosystem variables that can be described by a simple power function to make more generalized predictions about the role of hydrologic variability in influencing stream ecosystems.

[10] In general, we use this analysis to distinguish among ecological processes dominated by base flow

($Q_{eff}/Q_{mode} \sim 1$), moderate floods (i.e., recurrence interval of years, $Q_{eff}/Q_{mode} \sim 10-100$), and extreme floods (i.e., recurrence interval of decades to centuries, $Q_{eff}/Q_{mode} \sim 1000$). These results are used to examine how particular ecological variables are expected to vary spatially and temporally, and the effect of this variation on defining Q_{eff} for any given ecological variable. While Q_{eff} is shown to be a useful tool in analyzing stream ecosystems, there are ecological variables for which it is poorly suited, and we show how to identify those variables for which this analysis approach is most appropriate. We close with an examination of potential anthropogenic effects Q_{eff}, potential applications for river management, and potential future directions for research.

2. Methods

2.1. Analysis of Available Data

[11] Quantifying Q_{eff} for ecosystem processes first requires explicit knowledge of the relationship between some ecological variable and discharge (curve $S(Q)$ in Figure 1). Developing $S(Q)$ for geomorphology is relatively straightforward in that what matters is known; bed material load determines channel form, and the exponential shape of the geomorphic work function is consistent. In contrast, an array of ecological variables are influenced or governed to varying degrees by discharge, but also by other processes, such as temperature, sunlight, grazing, predation, and competition. Also, there are positive and negative feedbacks among ecological processes that make it more difficult to isolate the role of discharge. Thus we sought to analyze a range of response variables across different levels of ecological organization to provide an evaluation of possible ecological response to discharge.

[12] We searched published studies that related ecological variables directly to discharge and then analyzed these data to calculate Q_{eff}. The analysis also requires long-term hydrologic data to develop a frequency distribution curve. With the exception of physical habitat data from incremental flow methodology, relatively few ecological data sets met both of these criteria. A subset of qualifying data sets was selected to arrive at a final list that represented the best available variety of ecological variables. The variables analyzed are (1) organic matter transport, (2) algal growth, (3) transport of macroinvertebrates by floods, (4) nutrient transport and retention, and (5) physical habitat availability.

2.1.1. Ecological Variables Analyzed

[13] At the ecosystem level, organic matter (OM) transport and algal growth are core components of a stream's energy balance and provide valuable information for understanding food web dynamics. Nutrient transport and retention also represent fundamental ecosystem attributes and retention is now a widely used metric to illustrate within- and between-system differences in nutrient cycling in streams [*Fisher et al.*, 2004]. While several studies have related these variables to discharge [e.g., *Fisher and Likens*, 1972; *Webster*, 1983; *Butturini and Sabater*, 1998], few have taken the next step to place these relationships in the context of the stream's naturally varying discharge regime [*Fisher et al.*, 2004].

[14] Algal growth, transport of macroinvertebrates by spates, and habitat availability provide different measures of organismal-level responses to discharge. Understanding the role of disturbance (most often flooding) in shaping population and community dynamics has been an important research avenue in stream ecology over the past decade (e.g., see review by *Resh et al.* [1988]), but these studies typically emphasize either the response to individual floods [e.g., *Fisher et al.*, 1982; *Imbert and Perry*, 2000] or the relationship between disturbance frequency and biotic response [e.g., *Townsend et al.*, 1997]. Our goal is to link response variables to the entire range of a stream's discharge rather than focusing exclusively on extreme events.

[15] Finally, the effect of discharge variation on hydraulically defined habitat availability is the most widespread approach used in environmental flow analyses worldwide [*Tharme*, 2003]. Typically, such studies employ hydraulic models to assess the distribution of depth, velocity, and to a lesser extent, substrate and cover as functions of discharge. Ecosystem responses in terms of fish population or community metrics are then related empirically to indices calculated from the physical habitat variables [*Peterson and Rabeni*, 2001; *Tharme*, 2003]. Thus inventories of physical habitat (i.e., depth and velocity) known to be important for specific biota are used as a surrogate for direct examination of population or community dynamics. Discharge-habitat relations, $S(Q)$, then can be modeled to calculate Q_{eff} of habitat availability. The validity of this approach in describing habitat availability depends entirely on how well the hydraulic units identified describe biologically important habitat constraints.

[16] Some ecological variables are better suited to the effective discharge analysis than others. This limitation, and other limitations of our analytical approach are discussed at greater length below.

2.1.2. Analysis Methods

[17] The same analytical methods were followed for each variable, and specific details for the analysis are provided in the appendices in the auxiliary material.[1] Sources of ecological data are listed in Table 1. Hydrologic data for each of the study sites were obtained from historic data sets, and mean daily discharge was used in all cases to develop the hydrologic frequency distribution. All hydrologic data available in the records were used even though the published study may have collected ecological data for only a period of time within the entire hydrologic data set time period. Each hydrologic data set was divided into 25 logarithmically distributed bins and then the hydrologic frequency distribution was used to compute the portion of time the flow was within the discharge bin. This generated $f(Q)$ in Figure 1. Using a logarithmic distribution of discharge bins provides a more representative distribution from which to calculate the effective discharge than arithmetically distributed bins, which underemphasizes smaller, more frequent discharges likely to be important for ecological processes.

[18] For each of the discharge bins, the published relationship was used to link the ecological variable to the specific discharge bin to generate the $S(Q)$ curve, where $S(Q)$ represents the discharge dependence of the ecological

[1] Auxiliary material is available at ftp://ftp.agu.org/apend/wr/2005WR004222.

Table 1. Summary of Results of Effective Discharge Analysis

Ecological Variable	Site	Study	Mean Daily Q, m^3/s	Q_{mode}, m^3/s	Q_{eff}, m^3/s	Q_2, m^3/s	μ	σ	b
POM	Ichawaynochaway Ck, GA	*Golladay et al.* [2000]	22	15	57	144	2.8	0.8	1.5
CPOM winter	Big Hurricane Br, NC	*Webster* [1983]	0.074	0.067	0.084	0.20	−2.7	0.3	1.8
CPOM summer	Big Hurricane Br, NC	*Webster* [1983]	0.051	0.048	0.18	0.14	−3.1	0.4	3.7
CPOM late summer	Big Hurricane Br, NC	*Webster* [1983]	0.042	0.039	0.050	0.12	−3.3	0.5	2.1
CPOM leaf fall	Big Hurricane Br, NC	*Webster* [1983]	0.053	0.054	0.080	0.16	−3.1	0.5	2.2
CPOM	Bear Brook, NH	*Fisher and Likens* [1973]	0.0037	0.0010	0.021	0.071	−6.8	1.9	1.3
FPOM	Bear Brook, NH	*Fisher and Likens* [1973]	0.0037	0.0010	0.088	0.071	−6.8	1.9	1.4
DOM	Bear Brook, NH	*Fisher and Likens* [1973]	0.0037	0.0010	0.021	0.071	−6.8	1.9	1.1
CPOM	Bear Brook, NH	*Meyer and Likens* [1979]	0.0037	0.0010	0.021	0.071	−6.8	1.9	1.3
FPP winter	Bear Brook, NH	*Meyer and Likens* [1979]	0.0048	0.0012	0.034	0.068	−6.1	1.1	1.4
FPP summer	Bear Brook, NH	*Meyer and Likens* [1979]	0.0016	0.00042	0.045	0.027	−8.2	2.2	1.7
P retention	Bear Brook, NH	*Meyer and Likens* [1979]	0.0037	0.0010	0.0010	0.071	−6.8	1.9	N/A
DOC	Sycamore Ck, AZ	*Jones et al.* [1996]	0.76	0.035	73	34	−4.2	3.2	0.9
Periphyton	Sycamore Ck, AZ	*Grimm and Fisher* [1989]	0.76	0.035	0.67	34	−4.2	3.2	N/A
NO_3 load	Gwynns Falls, MD	Baltimore Ecosystem Study	1.1	0.90	0.90	23	−0.4	0.8	0.7
PO_4 load	Gwynns Falls, MD	Baltimore Ecosystem Study	1.1	0.90	142	23	−0.4	0.8	1.8
SO_4 load	Gwynns Falls, MD	Baltimore Ecosystem Study	1.1	0.90	0.90	23	−0.4	0.8	0.8
Invertebrate dist	Wilson Ck, Manitoba	*Cobb et al.* [1992]	0.156	0.0060	0.049	3.6	−3.2	1.7	N/A
Pool habitat	Bear Ck, AR	*Reuter et al.* [2002]	3.0	1.8	1.8	84	−0.1	1.4	N/A
Riffle habitat	Bear Ck, AR	*Reuter et al.* [2002]	3.0	1.8	3.2	84	−0.1	1.4	N/A
Habitat diversity	Bear Ck, AR	*Reuter et al.* [2002]	3.0	1.8	0.41	84	−0.1	1.4	N/A

variable. Only relationships for $S(Q)$ which were published and statistically significant were used for rating curves. The product of $f(Q)$ and $S(Q)$ produces the effectiveness curve, $E(Q)$, the peak of which is the ecologically effective discharge. Borrowing from the terminology of fluvial geomorphology, this final curve is an expression of "ecological work" done by flow for the target variable.

[19] The first analysis is a simple case of particulate organic matter (POM) transport data from *Golladay et al.* [2000] for Ichawaynochaway Creek, a fifth-order stream in Georgia (Appendix A). Seasonal effects on loading and subsequent transport of organic matter are often quite strong, so a single measure of organic matter transport and discharge, as done by *Golladay et al.* [2000], is not sufficiently representative of temporal fluctuations that can dominate organic matter dynamics in forested stream ecosystems. Thus *Webster* [1983] developed season-specific coarse particulate organic matter (CPOM) rating curves for Big Hurricane Creek, a small headwater stream (~60 ha drainage area) in the Coweeta Hydrologic Laboratory in North Carolina. These data were used to calculate season specific values of Q_{eff} for CPOM (Appendix B).

[20] Data from multiple studies [*Fisher and Likens*, 1973; *Meyer and Likens*, 1979] from Bear Brook, New Hampshire, were used to investigate differences in Q_{eff} among organic matter size fractions (Appendix C). DOM curves from Hubbard Brook were then compared to those derived from Sycamore Creek, Arizona [*Jones et al.*, 1996] (Appendix D), to consider how discharge relations for a single variable can vary between streams with vastly different flow regimes.

[21] Effective discharge for solutes were investigated first by considering differences among different solutes, then by examining transport and retention of dissolved and particulate P fractions. Q_{eff} for NO_3, PO_4, and SO_4 were determined for Gwynns Falls at Villa Nova, Maryland (drainage area ~84 km^2), from the NSF-LTER Baltimore Ecosystem Study (Appendix E). Transport and retention relationships for different fractions of P were also derived from Bear Brook, New Hampshire [*Meyer and Likens*, 1979] (Appendix F).

[22] Unlike nutrients and organic matter, we found no long-term relationships quantitatively linking periphyton (benthic algae and associated microbial community) accumulation and discharge, which was needed to develop a periphyton effective discharge curve. Thus an approximate but realistic relationship was modeled using some available data and the periphyton accumulation model of *Hondzo and Wang* [2002] and tested using periphyton and hydrology data available for Sycamore Creek, Arizona (Appendix G). The modeled relationship provides a sense for how the effective discharge curve for periphyton is likely to differ from the previously developed curves.

[23] To quantify the potential changes of macroinvertebrates due to discharges, we used data from *Cobb et al.* [1992] relating the portion of invertebrates mobilized as a function of discharge in Wilson Creek, Manitoba, a fourth-order stream with drainage area of 22 km^2 (Appendix H). Finally, habitat-discharge relationships were developed for Bear Creek in the Ozark Highlands of northern Arkansas. Habitat availability as a function of discharge was delineated based on the hydraulics of flow as a function of discharge, primarily by delineating the channel on the basis of Froude number, a dimensionless hydraulic variable (see Appendix I) [*Reuter et al.*, 2002].

[24] In cases where the ecological variable increased monotonically as a function of discharge, we developed the relationship between the variable and discharge according to a power function

$$S = aQ^b \tag{1}$$

where S is the ecological variable of interest (e.g., CPOM), Q is discharge, and a and b are empirically fitted parameters. In cases where studies presented multiple relationships (e.g., to account for hysteresis effects), the simplest function which fit equation (1) was used. If relationships were given in alternative forms (e.g., poly-

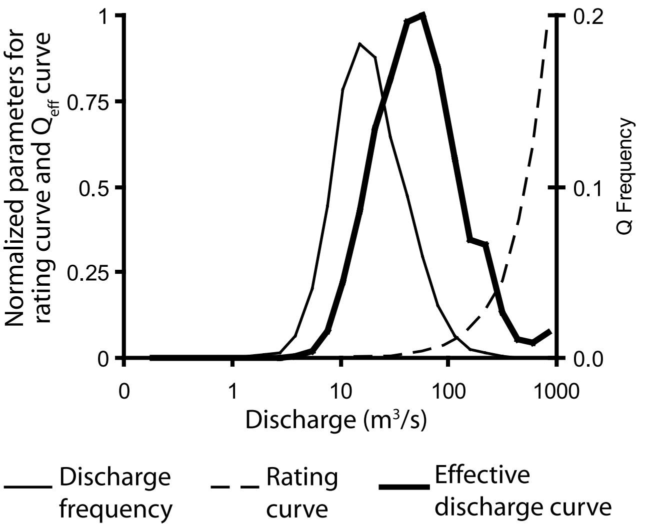

Figure 2. Effective discharge for particulate organic matter (POM) on Ichawaynochaway Creek, Georgia. Data are from *Golladay et al.* [2000].

nomials, log space), they were converted to a power function. This allowed direct comparisons among studies, and for the theoretical explorations discussed below.

[25] Once an effectiveness curve was generated, the peak of this curve was designated as the Q_{eff}, i.e., the most effective discharge. Some Q_{eff} curves had multiple modes, so the Q_{eff} was always identified as the maximum of the curve. Additionally, for each study we calculated the return interval for the 2 year flood event so that the Q_{eff} could be compared to the Q_2 (i.e., 2 year flood event), since the Q_2 is often roughly comparable to the geomorphic Q_{eff} [*Wolman and Miller*, 1960; *Andrews*, 1980] and is a general approximation of the bank-full discharge. We assumed a log Pearson type III frequency distribution for the annual series of peak flows [*Stedinger et al.*, 1992].

2.2. Model Development

[26] We developed an analytical relationship for effective discharges in cases where equation (1) applied to the ecological variable: all variables but periphyton accumulation, macroinvertebrate mobilization, and habitat availability. As a first approximation of hydrologic frequency, daily discharge was assumed to be lognormally distributed [*Stedinger et al.*, 1992; *Nash*, 1994]. The frequency of the mean daily discharge is then given by:

$$f(Q) = \frac{1}{Q\sigma\sqrt{2\pi}} e^{-\frac{(\ln Q - \mu)^2}{2\sigma^2}} \quad (2)$$

where μ and σ are the mean and the standard deviation of the logarithm of discharge, respectively. The effectiveness of a given discharge, the product of $f(Q)$ and S, is

$$E(Q) = \frac{aQ^b}{Q\sigma\sqrt{2\pi}} e^{-\frac{(\ln Q - \mu)^2}{2\sigma^2}} \quad (3)$$

The curve generated by equation (3) is the effective discharge curve (i.e., curve E in Figure 1), the peak of which is Q_{eff}. The actual effective discharge can be determined by setting the derivative of $E(Q)$ with respect to Q equal to zero and solving for Q, which can be approximated by [*Vogel et al.*, 2003]

$$Q_{eff} = e^{(b-1)\sigma^2 + \mu} \quad (4)$$

This equation is applicable to any ecological variable which can be described using the power function and if discharge can be described by a lognormal distribution. Note that μ is the modal discharge in ln space, and so e^{μ} is the modal arithmetic discharge; μ and σ can also be used with well-known transformations to compute the arithmetic mean and coefficient of variation of daily discharge at a site [*Vogel et al.*, 2003].

[27] To test this approach, values of ecological effective discharge were computed using the standard technique for variables described by power functions and the values predicted by equation (4). The advantage of using equation (4) is that it provides a quick approximation of the relative effects of hydrology (as reflected in the μ and σ terms) and ecology (reflected in the b term) on the approximate range of Q_{eff}, i.e., to rapidly approximate whether a particular ecological variable at a site is likely to be dominated by baseflow or rare floods.

3. Results and Discussion

3.1. Organic Matter Transport

3.1.1. Annual Organic Matter Loads

[28] Q_{eff} for POM on Ichawaynochaway Creek was 57 m^3/s (Figure 2), which was approximately 3 times the mean annual discharge (mean annual discharge = 21.6 m^3/s; Q_{mode} = 11 m^3/s), but only a fraction of the 2 year (bank-full) flood event (144 m^3/s). While floods are important in the transport of POM, as shown by the nonlinear increasing relationship between POM and Q (Figure 2), it is the discharges slightly larger than the mean daily discharge that are most effective for the export of organic matter over long periods of time.

3.1.2. Seasonal Variability

[29] Seasonal variability in Q_{eff} at Big Hurricane Branch was limited (Table 1 and Figure 3): Q_{eff} varied from 0.05 m^3/s in the late summer to 0.18 m^3/s in the early summer. While the winter had the highest mean daily discharge (0.074 m^3/s), it also had a relatively low exponent for the discharge-CPOM rating curve: the exponent b in equation (1) was 1.8 whereas all the other seasons had rating curve exponents greater than 2.1, with the early summer having the highest exponent of 3.7. In addition, while a narrow range of discharges was relatively effective for CPOM transport during the winter, a much wider range of flows was effective in other months, particularly during the early summer.

[30] Effective discharge for organic matter loads is determined jointly by the distribution of flows, the relative ease with which organic matter is transported by those flows within each season, and the availability of organic matter for transport. *Webster* [1983] suggested that in early summer, CPOM is more easily transported as it has been broken down over the winter (ease of entrainment) since initial leaf fall, resulting in the higher value for b in the early summer than in other months. Early summer months had a much

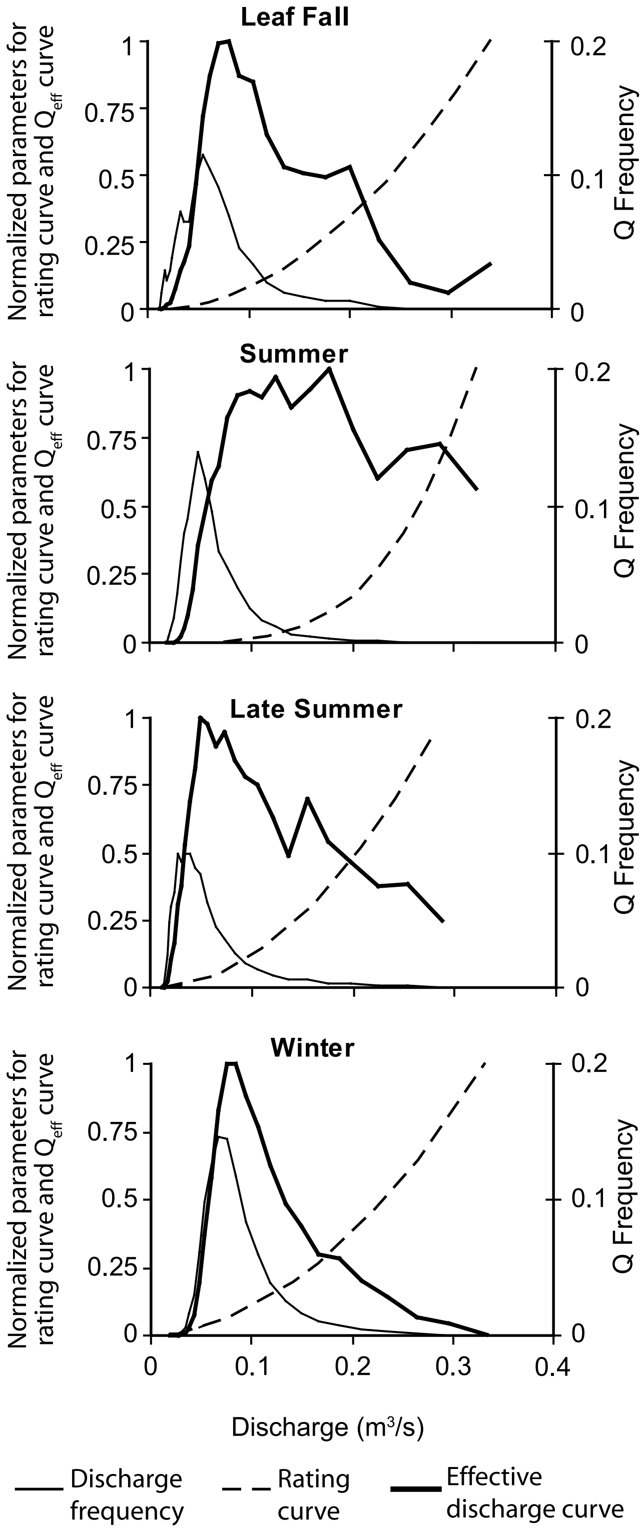

Figure 3. Variation in interseason effective discharge for coarse particulate organic matter (CPOM) on Big Hurricane Branch, Georgia. Data are from *Webster* [1983].

lower mean daily discharge than winter months, but this was compensated for by relatively large values for the exponent *b*, indicative of increased effectiveness of discharges during summer for the transport of CPOM. During winter months, formation of large leaf packs (high threshold of entrainment) limited the transport of CPOM despite the higher discharges during this season [*Webster*, 1983]. Thus CPOM transport in Big Hurricane Creek shows the discrepancy between the frequency of storm events (highest discharge in the winter months), and the magnitude of ecological work in the form of organic matter transport done by these events.

3.1.3. Effect of Organic Matter Size Fractions and Site

[31] As expected, Q_{eff} varied for the different size fractions of organic matter in Bear Brook: 0.021 m^3/s for CPOM and DOM, and 0.088 m^3/s for FPOM (Figure 4 and Table 1). For comparison, the mean daily discharge and Q_{mode} are 0.0037 and 0.001 m^3/s, respectively, and the Q_2 for Bear Brook is 0.071 m^3/s (Table 1). Thus the most

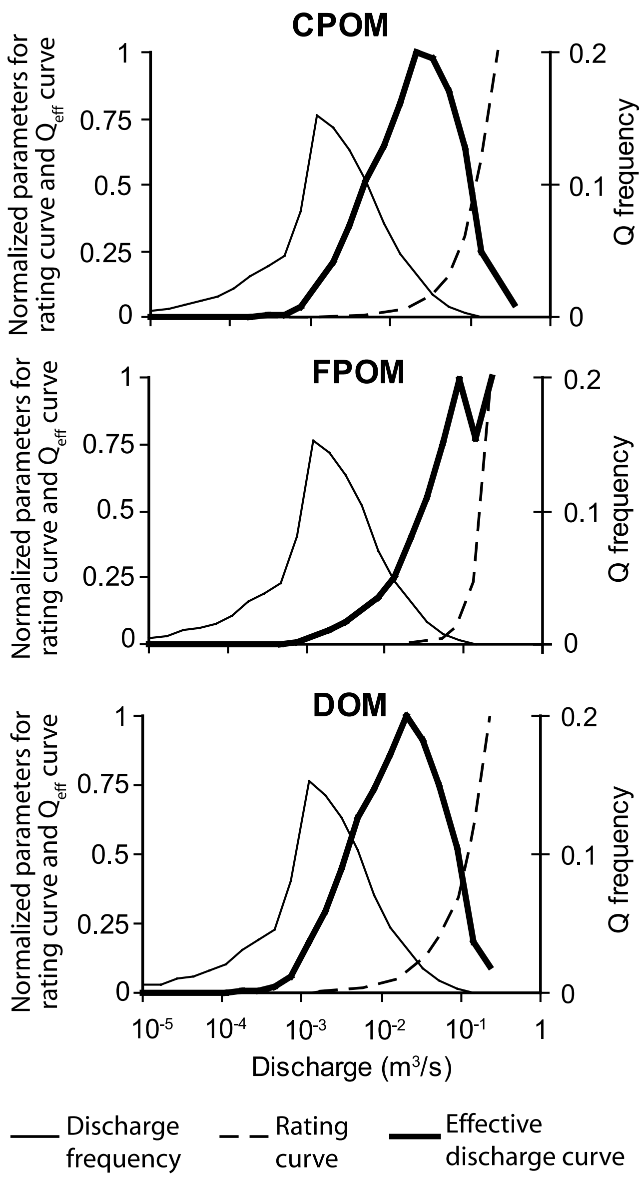

Figure 4. Variation in effective discharge among size fractions of organic matter on Bear Brook, New Hampshire, including coarse particulate organic matter (CPOM), fine particulate organic matter (FPOM), and dissolved organic matter (DOM). Data from *Fisher and Likens* [1973].

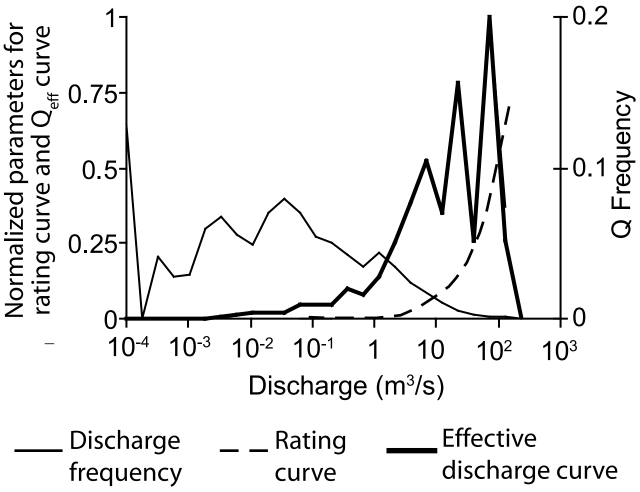

Figure 5. Effective discharge for dissolved organic carbon (DOC) on Sycamore Creek, Arizona. Data are from *Jones et al.* [1996].

effective discharge for all forms of organic matter in Bear Brook is moderate flood flows.

[32] In contrast to Bear Brook, Q_{eff} for DOC in Sycamore Creek, Arizona, was 73 m^3/s, which was substantially larger than the Q_{mean} (0.76 m^3/s) and Q_{mode} (0.035 m^3/s) (Figure 5 and Table 1). Whereas moderate flows were most effective for DOM at Bear Brook, very large and infrequent floods were most effective for DOC transport at Sycamore Creek (Figure 5 and Table 1). Indeed, the most effective discharge for DOC transport in Sycamore Creek was ~2000 times greater than the modal discharge, whereas Q_{eff} for DOM was within an order of magnitude of Q_{mode} for Bear Brook.

3.2. Nutrient Dynamics

3.2.1. Differences Among Solutes

[33] The Q_{eff} for PO_4 loads differed from those for NO_3 and SO_4 loads in Gwynns Falls, MD (Figure 6 and Table 1). Q_{eff} for both NO_3 and SO_4 loads was the same as the modal daily discharge, 0.9 m^3/s. Thus the modal discharge dominates the transport of NO_3 and SO_4 in this system. However, PO_4 transport was dominated by large discharges: the Q_{eff} was the largest flow of record, 142 m^3/s. The secondary mode in the Q_{eff} curve for PO_4 suggests that 21 m^3/s was also a highly effective discharge for the transport of PO_4. For comparison, Q_2 at this site is 23 m^3/s.

3.2.2. Measures of P Cycling

[34] *Meyer and Likens* [1979] showed that net phosphorus retention (portion of dissolved phosphorus retained) was inversely related to discharge, among other variables. That is, as discharge increased, less dissolved phosphorus was retained in their study reach; other studies have shown similar relationships [e.g., *Butturini and Sabater*, 1998; *Doyle et al.*, 2003]. Thus the fundamental relationship between this ecological variable (P retention) and Q is substantially different than for the previous cases.

[35] The most effective discharge for net phosphorus retention in Bear Brook was 0.001 m^3/s (Figure 7 and Table 1), which was comparable to the Q_{mode} (0.001 m^3/s). This was also comparable to the Q_{eff} for DOM at Bear Brook, but an order of magnitude less than the Q_{eff} for CPOM or FPOM (Figure 4 and Table 1). Thus frequent, low flows were most effective for net phosphorus retention in Bear Brook (see detailed discussion of effective discharge for nutrient retention by *Doyle* [2005]), which likely reflected greater opportunity for biotic uptake as well as greater sediment-water contact that fosters sorption of P on sediment surfaces.

[36] *Meyer and Likens* [1979] also quantified P export, which was predominantly in the form of fine particulate phosphorus (FPP). FPP transport was dominated by moderate flood flows: 0.034 m^3/s for Q_{eff} in the winter and 0.045 m^3/s in the summer (Figure 7 and Table 1). These discharges are 1 to 2 orders of magnitude greater than the

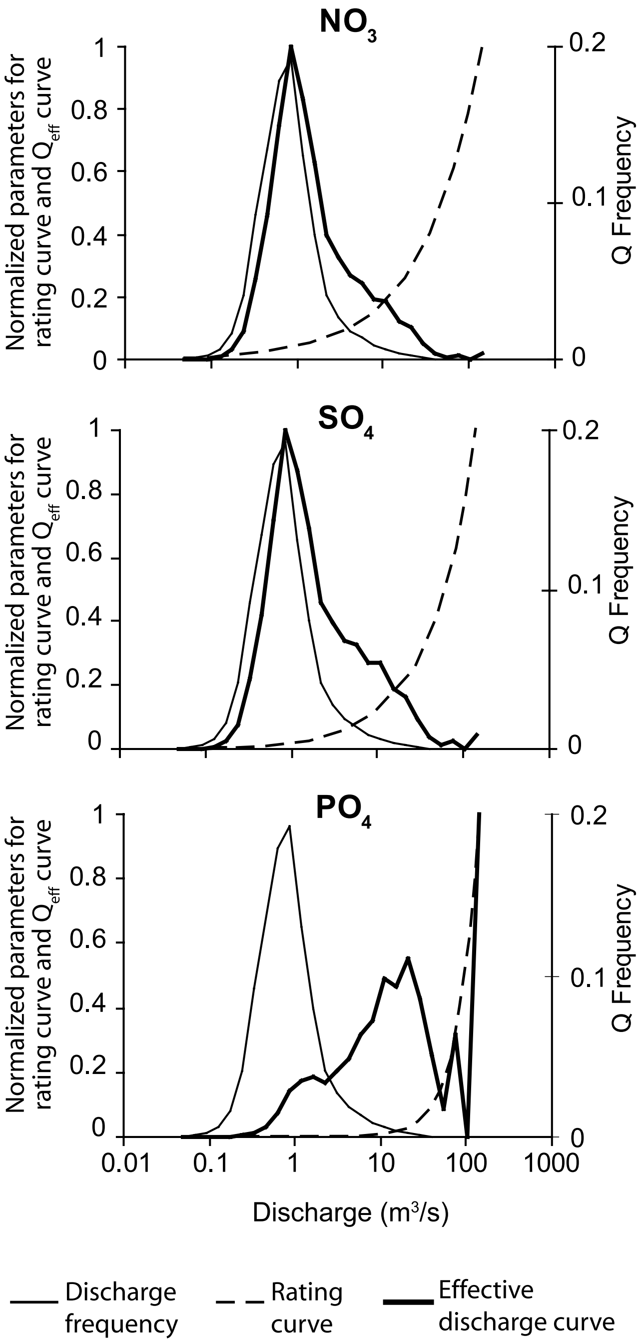

Figure 6. Effective discharge for nutrient loads on Gwynns Falls, Maryland. Data are from Baltimore Ecosystem Study [*Groffman et al.*, 2004].

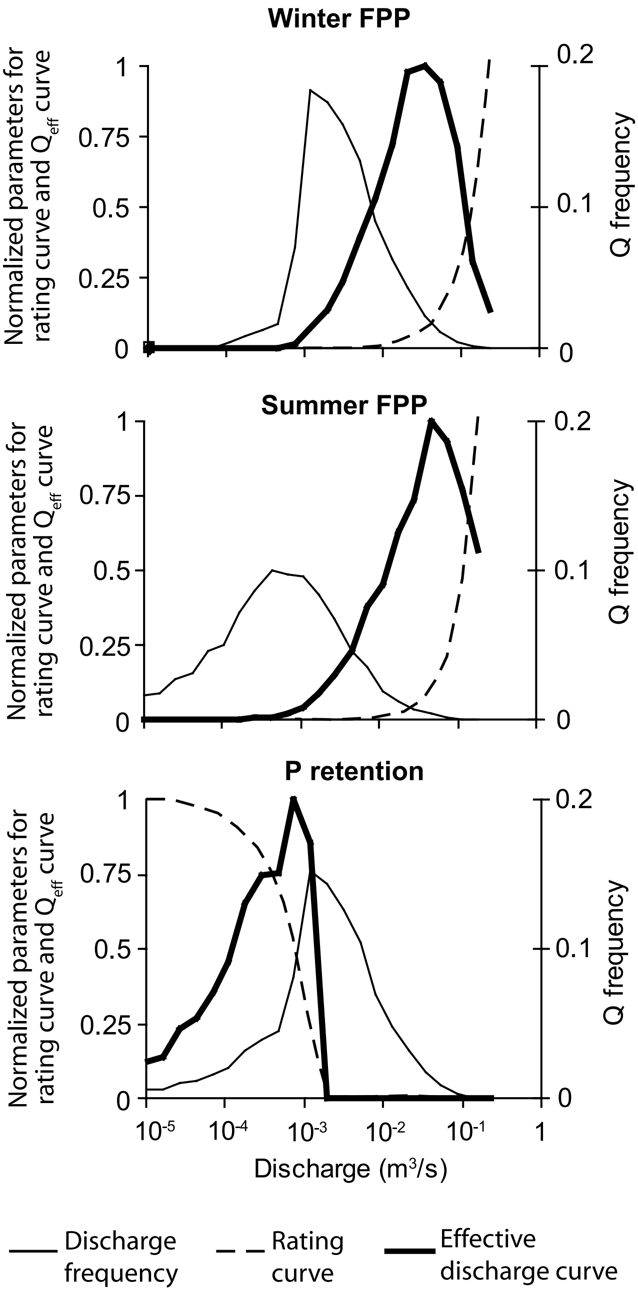

Figure 7. Effective discharge for dissolved phosphorus (P) retention and fine particulate phosphorus (FPP) transport on Bear Brook, New Hampshire. Data are from *Meyer and Likens* [1979].

modal discharge, and indicate that moderate floods are most effective at transporting FPP out of Bear Brook, driving the long-term FPP export budgets. Thus there were essentially two effective discharges for phosphorus dynamics in Bear Brook. Low flows dominate the accumulation or short-term retention of phosphorus, whereas moderate flood flows dominate the export of phosphorus. Meyer and Likens also showed that dissolved phosphorus retention in Bear Brook is temporary; over longer timescales the inputs and outputs of phosphorus balance. They showed that dissolved and coarse particulate phosphorus were the dominant inputs of phosphorus which were retained in the study reach, and our analysis shows that retention of these forms of P primarily occurred at low flows. Dissolved and coarse particulate phosphorus were converted into fine particulate phosphorus (FPP) over time, and that FPP made up the bulk of the exported phosphorus from Bear Brook [*Meyer and Likens*, 1979]. Thus both ranges of discharges were necessary for the current balanced P budget at Bear Brook.

3.3. Periphyton Growth and Removal

[37] The effective discharge for periphyton accumulation in Sycamore Creek, Arizona (0.67 m^3/s) was greater than the modal discharge, but almost the same as the mean daily discharge (0.76 m^3/s, Table 1 and Figure 8). For this desert stream, a wide range of discharges have comparable frequencies, leading to a relatively large difference between the modal discharge and the mean daily discharge (Table 1). This analysis also shows that there is a relatively limited discharge range that allows the greatest accumulation of periphyton on the channel bed: relatively small amounts of periphyton are accumulated at low discharges, but at large discharges, which occur infrequently, periphyton is removed via scour. This is in contrast to organic matter or nutrient loads in that while they have similar rarity of high flows, these loads are elevated at high flows rather than reduced.

[38] This value for Q_{eff} for periphyton is in stark contrast with the effective discharge for DOC of 73 m^3/s (Figure 5 and Table 1) at Sycamore Creek. This suggests that, like shown for Bear Brook, multiple discharges are effective for various ecological variables; low flows for periphyton accumulation in Sycamore Creek, high flows for DOC transport.

3.4. Macroinvertebrate Disturbances

[39] Unlike the earlier measures, the effective discharge curve for macroinvertebrate mobilization was distributed over a wide range of discharges, and slightly bimodal in Wilson Creek, Manitoba (Figure 9 and Table 1). The most effective discharge for invertebrate mobilization was

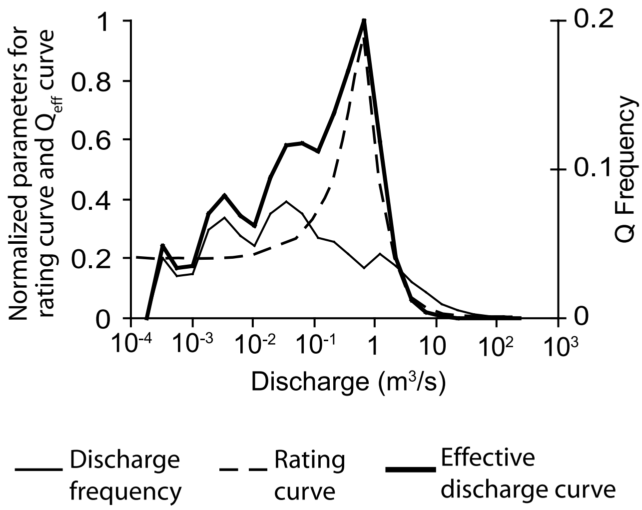

Figure 8. Effective discharge for periphyton growth and removal on Sycamore Creek, Arizona. Data are generated by simulation model, and calibration data are from *Grimm and Fisher* [1989].

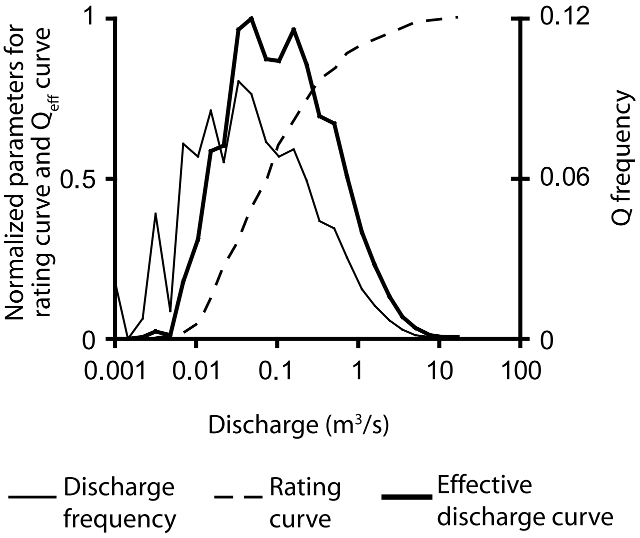

Figure 9. Effective discharge for macroinvertebrate mobilization on Wilson Creek, Manitoba, Canada. Data are from *Cobb et al.* [1992].

0.049 m^3/s, although there was a secondary mode in the effective discharge curve at 0.156 m^3/s. Thus the Q_{eff} was almost an order of magnitude larger than the Q_{mode}. This indicates that for Wilson Creek, a wide range of discharges are similarly effective in controlling the disturbance of invertebrates over time and that moderate floods are most effective at mobilizing macroinvertebrates.

3.5. Physical Habitat Availability

[40] Several types of $S(Q)$ curves result from the habitat class definitions and the hydraulic geometry of the Bear Creek; three of these are discussed here (Figure 10 and Table 1). Pools (slow, relatively deep water with low Froude numbers) initially increased in area as discharge increased to 1.8 m^3/s, then decreased until 10 m^3/s, and then subsequently expanded in area to a maximum at ca. 100 m^3/s. The two peaks of this relation were caused by the particular channel geometry of Bear Creek. The Q_{eff} curve showed that most of the available pool habitat was provided by moderate flows of 1.8 m^3/s. Units delineated as riffles, shallow, rapid flow with high Froude number, expanded monotonically with discharge because much of the channel was trapezoidal and maintained swift, relatively shallow water as flow increases. The riffle $S(Q)$ curve moved Q_{eff} for riffles to 2–5 m^3/s. We calculated habitat diversity using the Shannon-Wiener diversity index and found that habitat diversity increased gradually with discharge to peak at 0.5 m^3/s. Because the index varied little with discharge, Q_{eff} for habitat diversity was coincident with the peak of the discharge frequency distribution.

[41] Habitat $S(Q)$ curves and resultant Q_{eff} values are highly dependent on the specific hydraulic geometry of a river or stream and the criteria used to define physical habitat units. Many $S(Q)$ curves are peaked or complex and cannot be modeled as power functions, or other monotonic functions. Nevertheless, the Q_{eff} approach illustrates that different types of habitats can have substantially different Q_{eff} values, and that the long-term availability of these habitats is strongly governed by both hydrology frequency and habitat availability functions.

3.6. Modeling Results

[42] While geomorphic work is typically dominated by moderate flood flows, several ecological attributes are maximized at low flows, particularly flows within an order of magnitude of the modal daily discharge. What aspects of hydrology or ecology drive low-flow versus high-flow dependence, and what parameters can be used as indicators of what flows would dominate ecosystem processes? On the basis of the need for a power function relationship between ecological variables and discharge, equation (4) was not applicable to P retention, periphyton accumulation, invertebrate disturbance, or any of the habitat availabilities. These

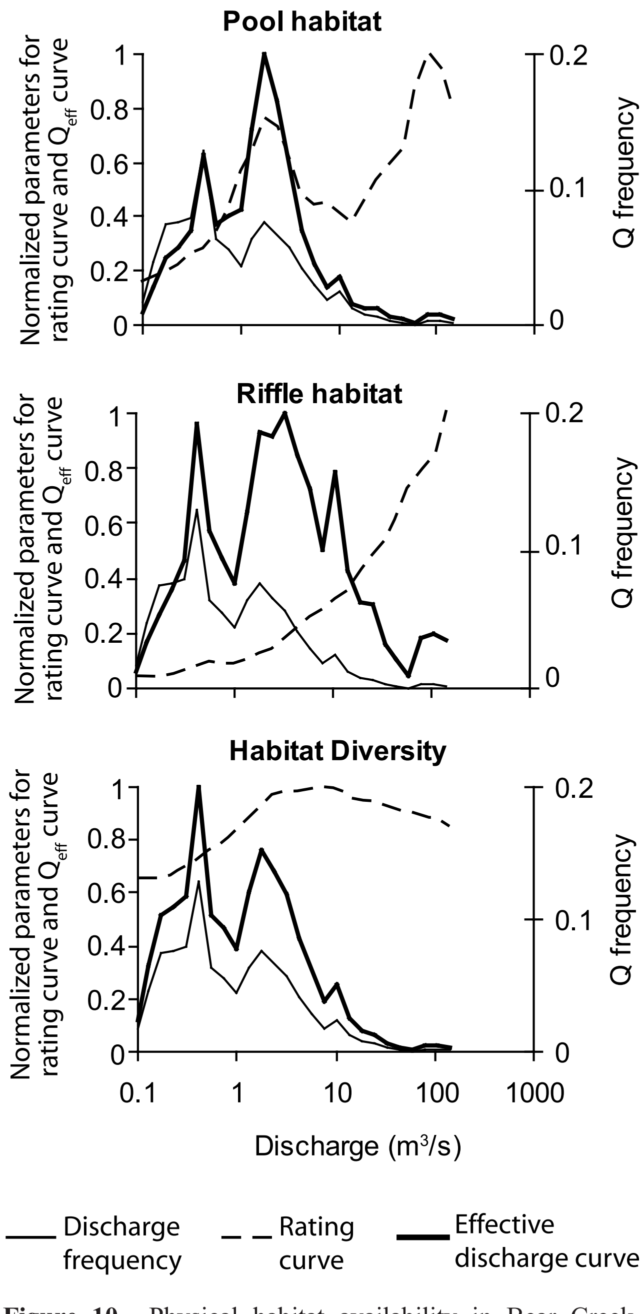

Figure 10. Physical habitat availability in Bear Creek, Arkansas. Data are from *Reuter et al.* [2002].

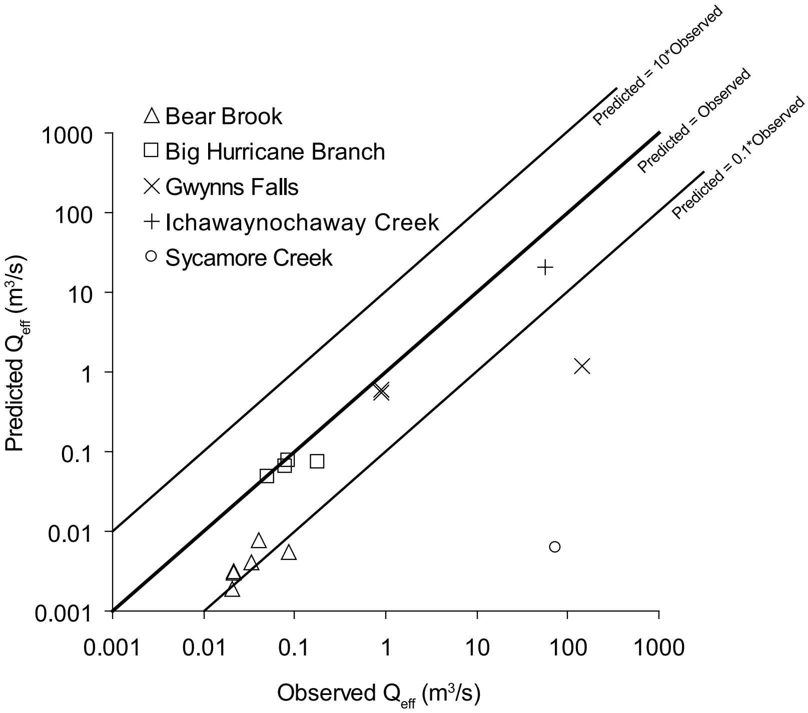

Figure 11. Theoretically derived Q_{eff} and observed Q_{eff} for ecological parameters that can be described by a power function. Thick diagonal line indicates theoretically predicted equals observed; other lines indicate one order of magnitude discrepancies between predicted and observed.

variables would need to be modeled with forms of $S(Q)$ other than a power function and examples are discussed below.

[43] Despite the generality of equation (4), predicted values of Q_{eff} matched the observed values fairly well, although there were outliers (PO_4 loads at Gwynn's Falls and DOC load at Sycamore Creek) for which the actual Q_{eff} was much greater than that predicted. However, the analytical expression (equation (4)) captured the main features of the effective discharge observed: all other predicted values of Q_{eff} were within an order of magnitude of the observed Q_{eff} (Table 1 and Figure 11, $p < 0.01$, $R^2 = 0.90$).

[44] Equation (4) reveals several interesting aspects of ecological effective discharge. First, the coefficient a does not appear in the equation, thus indicating that it is the degree of nonlinearity, expressed in exponent b, that controls the effective discharge. Second, this equation allows one to assess the necessary conditions for effective discharge to be near low, frequent discharges ($Q_{eff} \sim Q_{mode}$) or near rare floods ($Q_{eff} \gg Q_{mode}$). A limiting case occurs for an ecological variable that varied linearly with discharge, i.e., if the exponent b were 1. As $b \rightarrow 1$, then by equation (4), $Q_{eff} \rightarrow e^{\mu}$, or $Q_{eff} \rightarrow Q_{mode}$. Thus, for ecological processes that vary approximately linearly with flow, the most effective discharge can be approximated by the modal discharge. As b increases beyond 1, then $Q_{eff} > Q_{mode}$, and if $b < 1$ then $Q_{eff} < Q_{mode}$. For progressively larger values of $|b - 1|$, the Q_{eff} is essentially "pulled" away from Q_{mode}, toward larger discharges if $b > 1$, and toward smaller values if $b < 1$.

[45] As examples, the exponent b for NO_3 and SO_4 load curves for Gwynn's Falls were less than, but close to 1, while the b exponent for PO_4 was 1.8. Correspondingly, the Q_{eff} for NO_3 and SO_4 was the same as Q_{mode}, while Q_{eff} for PO_4 was orders of magnitude larger than Q_{mode} (Figures 6 and 12). The exponents for CPOM and FPOM at Bear Brook were 1.3 and 1.4, respectively, and all of the associated effective discharges were closer to moderate flood events than to the mean or modal discharge (Figures 4 and 12). Thus small changes in the b exponent can result in substantial changes in Q_{eff}. Coming back to sediment loads in river channels, exponents relating gravel sediment loads to discharge are often in the range of 2.3 to 5.1 [*Emmett and Wolman*, 2001], so effective discharge for gravel transport is most often associated with the 1.5+ year flood event, i.e., $Q_{eff} \gg Q_{mode}$.

4. General Discussion and Synthesis

[46] The concept of effective discharge has considerable potential to aid in the analysis and management of stream ecosystems, just as it has in geomorphology [e.g., *Shields et al.*, 2003]. Even for the simplest cases of ecological response to discharge (i.e., monotonically increasing, POM or nutrient loads), the high error in the relationship between the ecological variable and discharge will lead to high error in the estimates of Q_{eff} [*Benda et al.*, 2002]. Further, the application of effective discharge analysis in ecology will be more complex than in geomorphology, and the patterns of effectiveness curves will vary both across ecological variables and ecosystems. Nevertheless, the conceptual and analytical utility of the effective discharge analysis allows us to explore several general questions about how hydrologic variability influences various ecolog-

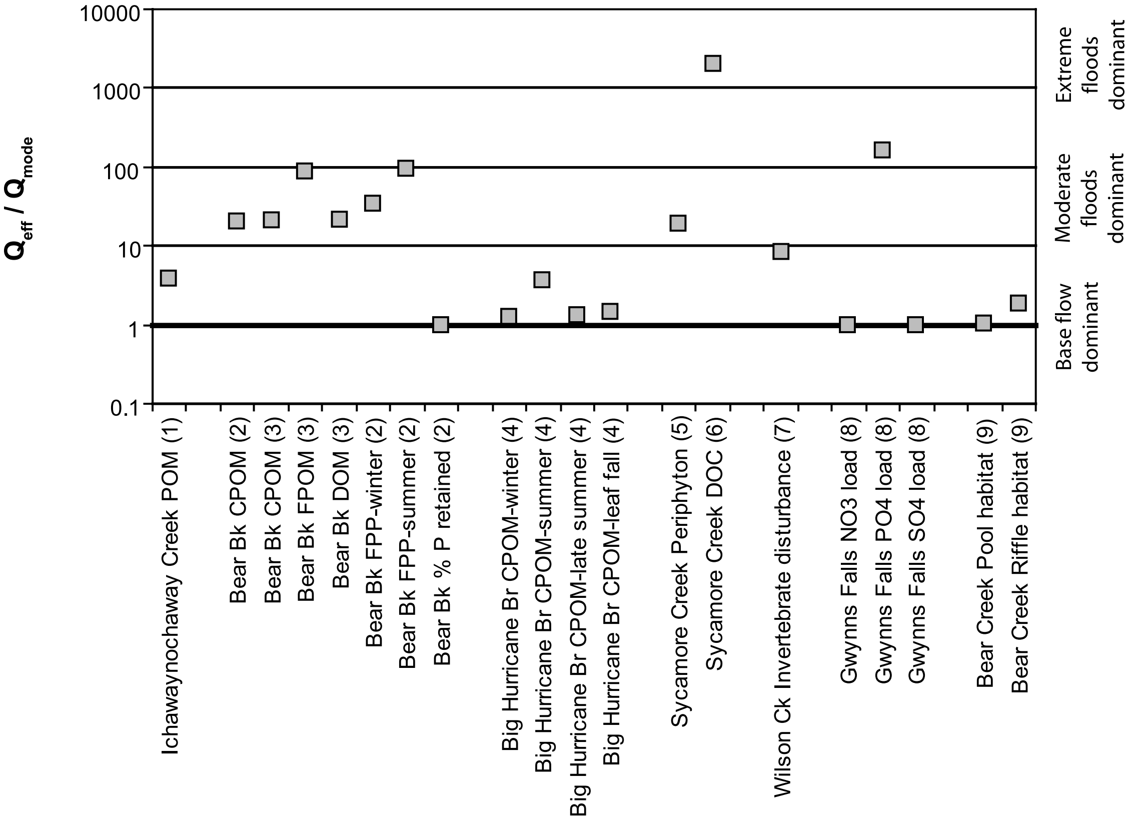

Figure 12. Relative values of Q_{eff} compared to Q_{mode}. Thick horizontal line indicates Q_{eff} values equal to Q_{mode}. References are as follows: 1, *Golladay et al.* [2000]; 2, *Meyer and Likens* [1979]; 3, *Fisher and Likens* [1973]; 4, *Webster* [1983]; 5, *Grimm and Fisher* [1989]; 6, *Jones et al.* [1996]; 7, *Cobb et al.* [1992]; 8, Baltimore Ecosystem Study (L. Band and P. Groffman, personal communication, 2004); 9, *Reuter et al.* [2002].

ical processes in streams. Given the uncertainty associated with the data contributing to the meta-analysis, the discussion below is focused on identifying the general range of flows that are most effective for a particular ecological variable rather than attempting to quantify a specific magnitude of flow that will dominate all ecological processes, i.e., identify what types of flows (extreme floods or common base flows) are most important for different ecological variables.

4.1. Single or Multiple Effective Discharges?

[47] The synthesis of the previous studies suggests that several discharges can be expected to be ecologically effective for a given stream (Figure 12). For example, the analysis of the Bear Brook data for phosphorus showed that both low flows and moderate floods maintained the phosphorus budget, with low flows dominating P retention and moderate floods maintaining the output, as FPP. In the absence of floods, then there may be a net accumulation of phosphorus, whereas chronic flooding may result in a depletion of P. Thus both ranges of discharges are necessary to maintain long-term nutrient balance [*Reddy et al.*, 1999].

[48] Across multiple sites, some ecological variables are driven by base flows or mean daily discharge (e.g., periphyton accumulation at Sycamore Creek, NO_3 or SO_4 loads at Gwynns Falls) while others primarily driven by moderate flood flows (e.g., CPOM export; PO_4 loads at Gwynns Falls). Thus, rather than a single effective discharge peak wherein a relatively narrow range of discharges dominates many processes, certain ecological processes are dominated by base flows ($Q_{eff}/Q_{mode} \sim 1$; e.g., NO_3 loads, periphyton accumulation, Bear Creek pool availability), others by moderate floods ($Q_{eff}/Q_{mode} \sim 100$; e.g., Bear Brook CPOM, Bear Creek riffle availability), while others driven by rare, extreme floods ($Q_{eff}/Q_{mode} \sim 1000$; e.g., Sycamore Creek DOC). The entire range of discharges will contribute to ecological change, with certain ecological variables being most influenced by particular portions of the hydrologic regime.

[49] It is particularly intriguing that there were differences in the types of flows that dominated the same variable at different sites. For instance, DOC was dominated by large, rare floods at Sycamore Creek, whereas DOM was dominated by only moderate, frequent floods at Bear Brook. This difference in Q_{eff} likely reflects contrasting sources of DOC at these two sites. DOC transport in Sycamore Creek is dominated by terrestrial inputs during flash floods and the dominance of extreme flows suggests an unusually high export of catchment NPP [*Jones et al.*, 1996]. Arid conditions limit both transport and decomposition of terrestrial OM, such that when a sufficiently large storm is finally able to move this material to the stream, the available terrestrial pool is substantial and thus results in high DOC concentrations and loads during the associated flood. In contrast, OM decomposition is an ongoing process in the mesic setting of Bear Brook, NH. Groundwater discharge and

Table 2. Types of Ecological Response Variables to Discharge

Ecological Response to Discharge	Description	Examples	Example Effectiveness Curves[a]	Applicability of Q_{eff} Analysis Approach
Transport	Discharge has primary and direct effect on these variables.	organic matter, nutrients, particles	13a–13c and 13e	high
Habitat	Discharge alters flow conditions for certain organisms and overall habitat size.	depth and velocity of flow	13f and 13h	high
Process modulation	Discharge indirectly regulates these variables and thus is correlated with them, but it is not a direct, deterministic link.	periphyton production, bivalve filtration, access to floodplain	13d, 13f, and 13g	moderate
Disturbance	Discharge is a reset mechanism.	macroinvertebrate mobilization	13f	low

[a]Effectiveness curves refers to the hypothetical curves in Figure 13.

slow decomposition of allochthonous OM provide a relatively constant source of DOC to this system, resulting in low-flow and moderate flood dominance.

[50] Results also indicate that high flows play a critical role in maintaining some ecological functions in streams. Discharges just at or above the bank-full discharge will likely be highly effective for an array of processes because these flows access the floodplain, increasing ecological processes associated with the capture of these additional habitats. Some examples include the addition of habitat for fish and phosphorus retention in alluvial floodplain rivers [*Welcomme*, 1979; *Olde Venterink et al.*, 2003]. Further, discharges that create boundary shear stresses near the critical value for sediment mobilization are also likely to be effective for several ecological processes, particularly rejuvenating in-channel habitat and disturbing macroinvertebrate communities [*Townsend et al.*, 1997].

[51] Thus effective discharge analysis provides a quantitative and mechanistic reinforcement of previous studies which emphasize the importance of hydrologic variability in streams [e.g., *Poff et al.*, 1997] and large rivers [*Jacobson and Galat*, 2005; *Power et al.*, 1995]. That is, to maintain ecological function in streams, an entire range of discharges is needed. In cases where flow is highly regulated, understanding of effective ecological discharges can provide a basis for target discharge regimes. In another sense, this is the danger of effectiveness, as some may see this as a call for one discharge when a wide range is needed. We will return to the potential applications of Q_{eff} below.

4.2. Types of Ecological Response to Discharge

[52] Our analysis suggests that the idea of effective discharge is useful in ecology, but empirical data are currently too scarce for us to describe all of the conditions under which this approach is applicable, or to lay out all of the possible functional relationships between discharge and ecological variables. Nevertheless, it is possible to sketch out the likely potential of effective discharge analysis in stream ecology.

[53] Discharge plays at least four distinct roles in stream ecosystems: material transport, habitat definition, process regulation, and disturbance. Each of these roles generates its own set of functional relationships with discharge, which determine the suitability and nature of effective discharge curves (Table 2 and Figure 13). Some of these roles generate essentially instantaneous relationships with discharge, while others are highly contingent, depending on past flow conditions, life history of organisms, or persisting conditions for some time into the future. Effective discharge analysis will perform well when there is a unique, essentially instantaneous relationship between discharge and an ecological process, and poorly when the discharge history has lags or legacy effects.

4.2.1. Discharge as Transport Mechanism

[54] Transport includes both particles and solutes. Particle concentrations (e.g., mass/volume) typically rise sharply with rising discharge, as water velocity and thus its competence to move particles rises. Hence particle load (mass/time) typically rises with discharge as a power function with an exponent $b > 1$, creating effective discharge greater than modal discharge (Figures 13a–13c). This is the basis of the geomorphic approach to effective discharge analysis, and seems to translate well to particle-associated materials in ecology (Figures 2–5 and 7). Two complications arise when considering the transport of particles in ecology. First, as seen in the case of CPOM (Figure 3), some groups of particles of ecological interest are very heterogeneous, and may have different transport properties in different times or places. Effective discharge analysis will be most useful in such cases if site- or season-specific information on particle transport can be obtained (e.g., Figure 3). Second, the geomorphic approach to particle transport assumes an infinite supply of particles and that sediment load is transport limited. If the particle pool is finite, i.e., supply limited, then the rating curve for particle transport may saturate (Figure 13e) or even decline at high discharge as the pool of transportable particles is exhausted [e.g., *Creed et al.*, 1996]. In such cases the concept of effectiveness remains applicable, but one cannot assume a simple monotonically increasing transport function.

[55] In the absence of anthropogenic alterations, most solutes arise from atmospheric sources or from weathering in the watershed. High runoff and commensurate high stream discharge usually mean less contact time between the water and soils in the watershed, so concentrations of many solutes arising from the watershed decline with rising discharge. This produces a rating curve for solute load that follows a power function with an exponent b that is slightly less than 1 (Figures 13a and 13b), and an effective discharge comparable to the modal discharge. Alternatively, if the solute originates from atmospheric deposition and is consumed by reactions in the watershed or stream channel (e.g.,

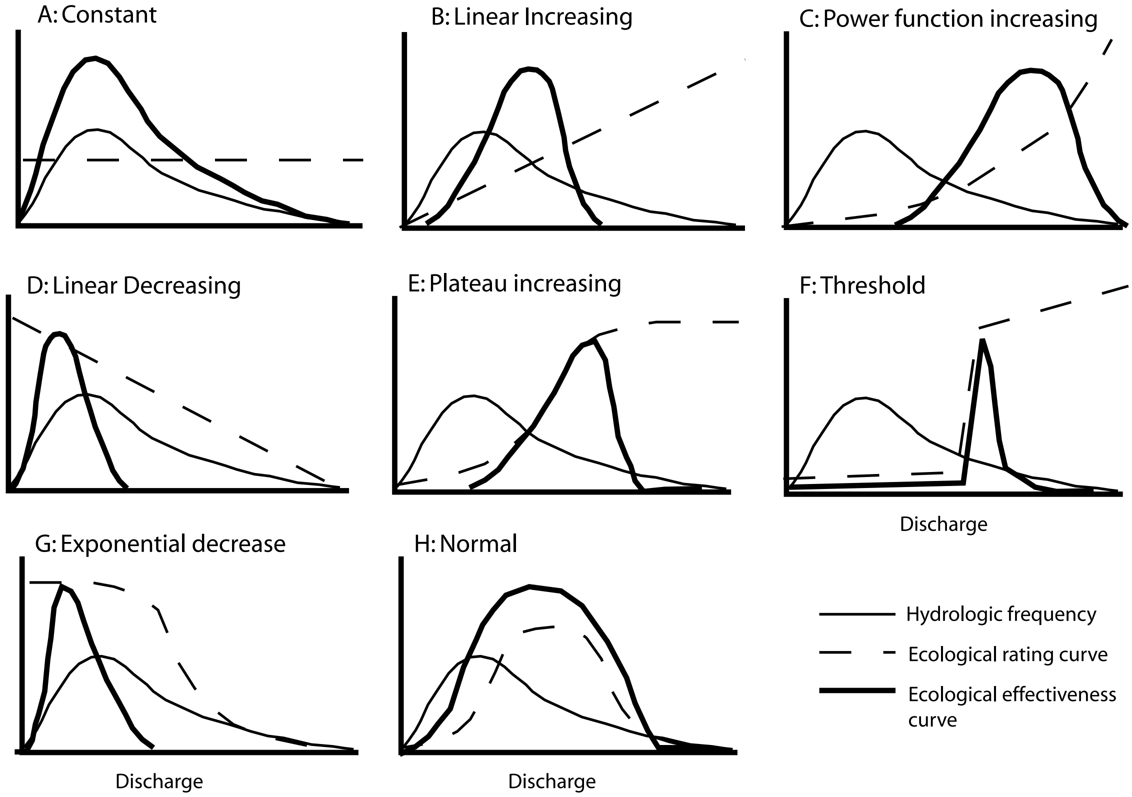

Figure 13. Hypothetical response curves for a variety of ecological variables. For potential ecological variables, see Table 2 and discussion in text.

H^+ and sometimes NO_3^-), lower contact times lead to concentrations that rise with discharge. The rating curve for transport load of these substances will have $b > 1$, and effective discharge will be greater than modal discharge (Figure 13c). Again, functional relationships may deviate from these ideals if limited supplies are exhausted at high discharge. On the basis of what is known about particle and solute transport in streams, and on the empirical analyses presented in this paper, effective discharge analysis will be a useful tool for the analysis of material transport in streams.

4.2.2. Discharge as a Regulator of Habitat

[56] Discharge defines the amount and character of habitat available in a stream by determining the size and location of the wetted volume, and the current speeds throughout that wetted volume. Analysis of ecological effective discharges requires knowing the function relating discharge to the amount or quality of habitat in the stream. Such functions may be unimodal or monotonic, but will certainly be idiosyncratic, depending on the site-specific details of channel morphology, as well as the needs of the organism. If such site-specific information is available, effective discharge analysis of habitat availability can produce useful insights. For instance, if the habitat-discharge function $S(Q)$ goes to zero at any value of Q, then the population will be extirpated or move elsewhere at a frequency equal to the return interval of that or more extreme flows. This estimate can then be compared with the colonization abilities of the species to assess the long-term viability of the population given a flow regime. Further, the area under the effective habitat curve $E(Q)$ provides an integrated measure of the goodness of the habitat given a flow regime. This measure could be used, for example, to assess the habitat value of various proposed flow regimes at a site.

[57] Effective discharge analysis will not work well to assess habitat if the organism is relatively immobile (e.g., rooted plants, mussels). The habitat requirement for an immobile organism is that a given area of stream be suitable at all discharges. Identifying and quantifying such areas requires information on the spatial arrangement of habitat suitability at every probable discharge, and thus a more sophisticated approach than effective discharge analysis.

4.2.3. Discharge as a Process Modulator

[58] Many ecological processes are regulated by discharge, either because they are regulated by current speed or by the accessibility of certain parts of the channel (e.g., the floodplain). Rising current speeds increase turbulence and thin boundary layers around solid objects, often stimulating processes such as nutrient uptake, primary production, and decomposition [e.g., *Hondzo and Wang*, 2002]. Because current speed at a site rises with discharge as a power function with an exponent $b \sim 0.4$ and ecological processes rise with current speed linearly or less than linearly (i.e., $b \sim 0$), such current-sensitive functions might be expected to follow power functions against discharge with exponents $b \sim 0.3-0.5$. In such cases, the ecologically effective discharge would be slightly less than but comparable to the modal discharge (equation (4)).

[59] Ecological processes may have other functional relationships with current speed. For instance, filtration rates of active suspension feeders such as bivalves are expected to follow a humped curve that peaks at intermediate current speeds [*Wildish and Kristmanson*, 1997]. This relationship will pull the ecologically effective discharge slightly below

or above the modal discharge, depending if the optimal current speed is less than or greater than the current speed at the modal discharge, respectively (Figure 13h).

[60] If ecological processes occur chiefly in a particular part of the channel, then there may be a threshold relationship between that process rate and discharge, as the water accesses that part of the channel. As discussed earlier, many processes (e.g., P retention in large rivers [*Olde Venterink et al.*, 2003] and spawning of many fish species [*Welcomme*, 1979]) occur chiefly on the floodplain. Such floodplain-dependent processes will have very steep ecological effectiveness curves, with effective discharges shifted far above modal discharges (Figure 13f).

4.2.4. Discharge as a Disturbance

[61] Finally, discharge is an agent of disturbance that affects many ecological variables. Disturbance (the removal of living biomass from a population) by high flows likely follows a steep power function ($b > 1$) or sigmoid curve (Figures 9, 13c, and 13e). In either case, the effective discharge (the one that kills or entrains the most organisms over the long term, given a flow regime) will be displaced well above the modal discharge. The effective discharge for disturbance may be a key discharge for understanding the effects of disturbance on the distribution and evolution of a species, as well as representing the outcome of evolutionary adaptations against disturbance. It also may be the appropriate discharge at which to look at issues like the spatial patterning of disturbance effects [e.g., *Strayer*, 1999].

[62] Two additional insights emerge from a effective discharge analysis of disturbance. First, if the population is small, a population will disappear if the disturbance (mortality) curve reaches any value m_q such that

$$\mathrm{N}\left(1 - \mathrm{m_q}\right) < \mathrm{N_{crit}} \tag{5}$$

where N is the population size before the disturbance, m_q is the mortality imposed by the disturbance, and N_{crit} is the minimum viable population size. Second, the population cannot persist if the summed mortality from disturbance is greater than the maximum achievable population growth rate in nature. Without considering the sequence of flows (see below), the population will disappear if

$$\int S(\mathrm{Q})\mathrm{f}(\mathrm{Q})\mathrm{dQ} > \lambda \tag{6}$$

where λ is the maximum achievable population growth rate in nature. Note that the population may not persist even if this condition is not met because of mortality from other sources (e.g., predators) or because population growth rates are below optimal.

[63] Very low flows may also represent an important ecological disturbance. Again, it seems likely that the functional relationship will be a steep power curve (but this time with $b \ll 0$) or reverse sigmoid curve, so that effective discharges fall well below modal discharges.

[64] Nevertheless, important effects of disturbance on stream ecosystems often persist for a very long time after the disturbance event [*Romme et al.*, 1998]. For example, extreme floods may result in physical or biological state changes that reorganize the system and reshape fundamental relationship between ecological processes and discharge. Effective discharge analysis will not be suitable for addressing the persistent effects of disturbance, because current ecological conditions depend so strongly on the past sequence of flow events and ecological responses, not simply the instantaneous discharge. Likewise, it is not prudent to interpret the area under the effective disturbance curve as the total mortality induced by a flow regime, because actual mortality will depend on the timing and sequence of flows, not simply on the distribution of flows.

4.3. Spatial Predictions and Effects of Land Use Change

[65] In addition to analyzing the relative effective discharges of ecological processes at a particular site, this analysis allows qualitative predictions of how effective discharge should vary systematically through a watershed and the potential effects of climate or land use change. This is easily done by using equation (4) and the hydrologic metrics of μ and σ to quantify hydrologic variability (Table 1). For example, Ichawaynochaway Creek is a fourth-order river in the southeastern US (Georgia), with $\mu = 2.8$ ($Q_{mode} = 20$ m^3/s) and $\sigma = 0.8$. In contrast, Bear Brook is a second- and third-order stream in the northeastern US (New Hampshire) with $\mu = -6.8$ ($Q_{mode} = 0.001$ m^3/s) and $\sigma = 1.9$, indicating the smaller mean and greater variability associated with headwater catchments. Sycamore Creek (Arizona) is a fourth-order arid stream with $\mu = -4.2$ ($Q_{mode} = 0.035$ m^3/s) and $\sigma = 3.2$, indicating the relatively low mode but high variability associated with large, arid watersheds.

[66] Small changes in σ can have a relatively large impact on Q_{eff} since σ is squared in equation (4). Equation (4) suggests that for $b > 1$, σ increases will result in Q_{eff} increases. Thus, for a given modal discharge, streams with flashy hydrology will have greater Q_{eff} than those with less flashy hydrology. On the basis of this logic, effective discharges should be skewed toward higher discharges in urban and arid watersheds. Second, equation (4) allows approximating systematic variability in Q_{eff} through a watershed. Within a physiographic region, μ and σ are often inversely related [*Vogel et al.*, 2003]; upstream rivers have smaller discharges than downstream rivers ($\mu_{\mathrm{upstream}} < \mu_{\mathrm{downstream}}$), but upstream, smaller rivers have greater hydrologic variability than downstream, larger rivers ($\sigma_{\mathrm{upstream}} > \sigma_{\mathrm{downstream}}$). Therefore, for a given value of b, Q_{eff} in larger channels will be associated with more frequent, mean discharges than in smaller, headwater channels.

4.4. Limitations of Approach

[67] While the effective discharge concept has enjoyed much success in fluvial geomorphology, it has some critics. There is a continued debate on the role of extremely large floods on dominating channel morphology [*Phillips*, 2002] and long-term sediment loads [*Vogel et al.*, 2003]. Further, many geomorphologists object to the inherent assumption of geomorphic equilibrium in applying the effective discharge concept [*Richards*, 1999]. Despite this, the importance of the effective discharge concept as a cornerstone of current geomorphic thinking cannot be ignored [*Doyle and Julian*, 2005], nor can its use as a widely applied analytical tool, particularly in the burgeoning field of river restoration [*Shields et al.*, 2003].

[68] Unlike the case of geomorphology where sediment rating curves can be generalized as power functions, many ecological variables lack direct relationships to discharge, and in cases where ecological variables can be linked to discharge, standard errors of prediction are often large. Rating curves can vary from highly significant to completely insignificant, and many studies have shown hydrologic parameters other than discharge magnitude to be highly influential for stream ecosystems [*Poff et al.*, 1997]. Finally, in the case of solute transport, while a positive relationship between discharge and a response variable (e.g., PO_4 retention) provides useful information about that solute, it is important to recognize the limitations on this information. A positive discharge-retention relationship does not identify the specific processes at work (for example, whether PO_4 is retained by biotic uptake or sorption), and it speaks to only one phase of the element's cycle. Further, it is information about just one part of the larger solute cycle and that other parts of the cycle may be controlled by processes that are not discharge-dependent. Therefore these relationships emphasize movement and storage of particular forms of a solute, and not the entire element cycle. However, the effective discharge concept remains a highly useful analytical tool that explicitly and quantitatively couples ecosystem processes with hydrologic variability. In addition to providing the broad hydrologic context for examining ecological variables, this approach draws explicit attention to the strength and shape of the relationship between discharge and the response variable of interest. From a practical perspective, the modeling results presented above show that Q_{eff} is highly dependent on the b value. These rating curves are strongly influenced by extreme events, which are often not well represented in many sampling programs. A single extreme event may shift the b from <1, ($Q_{eff} \sim Q_{mode}$) to $b \gg 1$ ($Q_{eff} \gg Q_{mode}$). Thus failure to capture these extremes could lead to misunderstanding the effect of discharge on the ecological variable [*Phillips*, 2002; *Vogel et al.*, 2003].

4.5. Future Research Directions and Applications

[69] While the above analysis and modeling exercise provided intriguing results, they are not a sufficient test of the ecological effective discharge concept. Rather, a systematic evaluation of the concept at a single site for a range of ecological variables is needed. Our ability to confidently generalize our results was reduced by our having to use other studies' data, as well as the extreme diversity in study site hydrology. Applying the concept at a particular site across a range of ecological variables at that site would provide a more robust test of the viability of the approach for stream ecosystem analysis, followed by a similar study across a range of hydrologic variability. Alternatively, a single ecological variable could be examined across a range of hydrologic conditions. Indeed, this latter test could be easily conducted using the National Water Quality Assessment database through the U.S. Geological Survey in order to examine how Q_{eff} for nutrient loads varies across a wide range of conditions.

[70] There is also the intriguing potential application of the effective discharge concept to river management issues, to include other key ecological drivers, and to other ecosystems. This analysis approach would be particularly useful in comparing the long-term effects of flow modification, flow allocation, or channel reconfigurations for habitat restoration. For instance, on the lower Missouri River, habitat for the endangered pallid sturgeon (*Scaphirhynchus albus*) is limited by a combination of channelization and flow regulation. Altering channel morphology alone would alter the habitat-discharge rating curve, whereas altering discharge releases from upstream would affect the frequency distribution of flows, and a recent study analyzes the individual and combined effects of morphology and hydrology on lower Missouri River habitat availability [*Jacobson and Galat*, 2005]. The relative impacts of both of these on long-term habitat availability could be quantified using the Q_{eff} analysis. Channel and discharge could then be modified to optimize the expected habitat availability.

[71] While discharge is a master variable in streams, ecological patterns and processes are clearly affected by multiple drivers in addition to flow. For example, temperature also plays a central role for growth and life history attributes of many aquatic organisms [*Vannote and Sweeney*, 1980] and is often incorporated into process rate equations. In addition, other ecosystems are driven by disturbances analogous to floods in streams [*Fisher and Grimm*, 1991]. Thus, if a frequency distribution can be estimated for the disturbance of interest, and the relative amount of ecological work done by that disturbance magnitude can be estimated, then the same frequency magnitude analysis could be applied. Other salient examples might include ice storms or landslides in forested ecosystems.

5. Conclusions

[72] Over the past decade, ecologists have made great strides in understanding the fundamental importance of discharge in shaping ecological pattern and process in streams [*Power et al.*, 1995; *Poff et al.*, 1997]. Yet our understanding of the relationships between hydrology and ecological response tends to be qualitative and descriptive in nature [*Benda et al.*, 2002]. As both hydrologists and ecologists assist in environmental decision making, quantitative tools become increasingly necessary. Ecologists will likely be called upon to be specific and predictive about ecological response to management actions in the future, particularly as unique and sizable restoration opportunities arise (e.g., Missouri River restoration, Grand Canyon experimental floods, restoration of flows to the Everglades).

[73] Attributing many ecological processes to discharge regime is obviously a conceptual leap. Despite this, identification of the effective discharge is a powerful tool for analyzing stream ecosystems as it provides a quantitative mechanism of analyzing the combined effects of ecological processes and hydrologic variability.

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References

Andrews, E. D. (1980), Effective and bankfull discharges of streams in the Yampa River basin, Colorado and Wyoming, *J. Hydrol.*, *46*, 301–310.

Baker, V. R. (1977), Stream-channel response to floods, with examples from central Texas, *Geol. Soc. Am. Bull.*, *88*, 1057–1071.

Benda, L. E., N. L. Poff, C. Tague, M. A. Palmer, J. Pizzuto, S. Cooper, E. Stanley, and G. Moglen (2002), How to avoid train wrecks when using science in environmental problem solving, *BioScience*, *52*, 1127–1136.

Butturini, A., and F. Sabater (1998), Ammonium and phosphate retention in a Mediterranean stream: Hydrological versus temperature control, *Can. J. Fish. Aquatic Sci.*, *55*, 1938–1945.

Cobb, D. G., T. D. Galloway, and J. F. Flannagan (1992), Effects of discharge and substrate stability on density and species composition of stream insects, *Can. J. Fish. Aquat. Sci.*, *29*, 1788–1795.

Creed, I. F., L. E. Band, N. W. Foster, K. Morrison, J. A. Nicholson, R. S. Semkin, and D. S. Jeffries (1996), Regulation of nitrate-N release from temperate forests: A test of the N flushing hypothesis, *Water Resour. Res.*, *32*, 3337–3354.

Doyle, M. W. (2005), Incorporating hydrologic variability into nutrient spiraling, *J. Geophys. Res.*, *110*, G01003, doi:10.1029/2005JG000015.

Doyle, M. W., and J. Julian (2005), The most-cited works in geomorphology, *Geomorphology*, In press.

Doyle, M. W., E. H. Stanley, and J. M. Harbor (2003), Hydrogeomorphic controls on phosphorus retention in streams, *Water Resour. Res.*, *36*(6), 1147, doi:10.1029/2003WR002038.

Emmett, W. W., and M. G. Wolman (2002), Effective discharge and gravel-bed rivers, *Earth Surf. Processes Landforms*, *26*, 1369–1380.

Fisher, S. G., and N. B. Grimm (1991), Streams and disturbance: Are cross-ecosystem comparisons useful?, in *Comparative Analyses of Ecosystems: Patterns, Mechanisms and Theories*, edited by J. J. Cole, G. M. Lovett, and S. E. G. Findlay, pp. 196–221, Springer, New York.

Fisher, S. G., and G. E. Likens (1973), Energy flow in Bear Brook, New Hampshire: An integrative approach to stream ecosystem metabolism, *Ecol. Monogr.*, *43*, 421–439.

Fisher, S. G., L. J. Gray, N. B. Grimm, and D. E. Busch (1982), Temporal succession in a desert stream following flash flooding, *Ecol. Monogr.*, *52*, 93–110.

Fisher, S. G., R. A. Sponseller, and J. B. Heffernan (2004), Horizons in stream biogeochemistry: Pathways to progress, *Ecology*, *85*, 2369–2379.

Golladay, S. W., K. Watt, S. Entrekin, and J. Battle (2000), Hydrologic and geomorphic controls on suspended particulate organic matter concentration and transport in Ichawaynochaway Creek, Georgia, USA, *Arch. Hydrobiol.*, *149*, 655–678.

Grimm, N. B., and S. G. Fisher (1989), Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream, *J. N. Am. Benthol. Soc.*, *8*, 283–307.

Groffman, P. M., N. L. Law, K. T. Belt, L. E. Band, and G. T. Fisher (2004), Nitrogen fluxes in urban watershed ecosystems, *Ecosystems*, *7*, 393–403.

Hondzo, M., and H. Wang (2002), Effects of turbulence on growth and metabolism of periphyton in a laboratory flume, *Water Resour. Res.*, *38*(12), 1277, doi:10.1029/2002WR001409.

Imbert, J. B., and J. A. Perry (2000), Drift and benthic invertebrate responses to stepwise and abrupt increases in non-scouring flow, *Hydrobiologia*, *436*, 191–208.

Jacobson, R. B., and D. L. Galat (2005), Flow and form in rehabilitation of large-river ecosystems–An example from the lower Missouri River, *Geomorphology*, in press.

Jones, J. B., Jr., S. G. Fisher, and N. B. Grimm (1996), A long-term perspective of dissolved organic carbon transport in Sycamore Creek, Arizona, USA, *Hydrobiologia*, *317*, 183–188.

Meyer, J. L., and G. E. Likens (1979), Transport and transformation of phosphorus in a forest stream ecosystem, *Ecology*, *60*, 1255–1269.

Nash, D. B. (1994), Effective sediment-transporting discharge from magnitude-frequency analysis, *J. Geol.*, *102*, 79–95.

Olde Venterink, H., F. Wiegman, G. E. M. Van der Lee, and J. E. Vermaat (2003), Role of active floodplains for nutrient retention in the Rhine River, *J. Environ. Qual.*, *32*, 1430–1435.

Peterson, J. T., and C. F. Rabeni (2001), The relation of fish assemblages to channel units in an Ozark stream, *Trans. Am. Fish. Soc.*, *30*, 911–926.

Phillips, J. D. (2002), Geomorphic impacts of flash flooding in a forested headwater basin, *J. Hydrol.*, *269*, 236–250.

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

Power, M. E., A. Sun, G. Parker, W. E. Dietrich, and J. T. Wootton (1995), Hydraulic food-chain models, *BioScience*, *456*, 159–167.

Reddy, K. R., R. H. Kadlec, E. Flaig, and P. M. Gale (1999), Phosphorus retention in streams and wetlands: A review, *Crit. Rev. Environ. Sci. Technol.*, *29*, 433–455.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. Wissmar (1988), The role of disturbance in stream ecology, *J. N. Am. Benthol. Soc.*, *7*, 433–455.

Reuter, J. M., R. B. Jacobson, and C. M. Elliott (2002), Physical stream habitat dynamics in lower Bear Creek, northern Arkansas, *Biol. Sci. Rep. USGS/BRD/BSR-2002-0002*, 113 pp., U.S. Geol. Surv., Washington, D. C.

Richards, K. (1999), The magnitude-frequency concept in fluvial geomorphology: A component of a degenerating research programme?, *Z. Geomorphol.*, *115*, 1–18.

Romme, W. H., E. H. Everham, L. E. Frelich, M. A. Moritz, and R. E. Sparks (1998), Are large, infrequent disturbances qualitatively different from small, frequent disturbances?, *Ecosystems*, *1*, 524–534.

Shields, F. D., R. R. Copeland, P. C. Klingeman, M. W. Doyle, and A. Simon (2003), Design for stream restoration, *J. Hydraul. Eng.*, *129*, 575–584.

Stedinger, J. R., R. M. Vogel, and E. Foufoula-Georgiou (1992), Frequency analysis of extreme events, in *Handbook of Hydrology*, edited by D. Maidment, pp. 18.1–18.66, McGraw-Hill, New York.

Strayer, D. L. (1999), Use of flow refuges by unionid mussels in rivers, *J. N. Am. Benthol. Soc.*, *18*, 468–476.

Tharme, R. E. (2003), A global perspective on environmental flow assessment: Emerging trends in the development and application of environmental flow methodologies for rivers, *River Res. Appl.*, *19*, 397–441.

Townsend, C. R., M. R. Scarsbrook, and S. Dolédec (1997), Quantifying disturbance in relation to macroinvertebrate species traits and species richness, *J. N. Am. Benthol. Soc.*, *16*, 531–544.

Vannote, R. L., and B. W. Sweeney (1980), Geographic analysis of thermal equilibria: A conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities, *Am. Nat.*, *115*, 667–695.

Vogel, R. M., J. R. Stedinger, and R. P. Hooper (2003), Discharge indices for water quality loads, *Water Resour. Res.*, *39*(10), 1273, doi:10.1029/2002WR001872.

Webster, J. R. (1983), The role of benthic macroinvertebrates in detritus dynamics of streams: A computer simulation, *Ecol. Monogr.*, *53*, 383–404.

Welcomme, R. L. (1979), *Fisheries Ecology of Floodplain Rivers*, Longman, New York.

Wildish, D., and D. Kristmanson (1997), *Benthic Suspension Feeders and Flow*, Cambridge Univ. Press, New York.

Wolman, M. G., and J. P. Miller (1960), Magnitude and frequency of forces in geomorphic processes, *J. Geol.*, *68*, 54–74.

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