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The influence of relative sediment supply on riverine habitat heterogeneity

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Abstract

The diversity of aquatic habitats in streams is linked to physical processes that act at various spatial and temporal scales. Two components of many that contribute to creating habitat heterogeneity in streams are the interaction between sediment supply and transport capacity and the presence of local in-stream structures, such as large woody debris and boulders. Data from previously published flume and field studies and a new field study on tributaries to the South Yuba River in Nevada County, California, USA, were used to evaluate the relationship between habitat heterogeneity, local in-stream structural features and relative sediment supply. Habitat heterogeneity was quantified using spatial heterogeneity measures from the field of landscape ecology. Relative sediment supply, as expressed by the sediment supply/transport capacity ratio, which controls channel morphology and substrate textures, two key physical habitat characteristics, was quantified using a dimensionless bedload transport ratio, q^*. Calculated q^* values were plotted against an ecologically meaningful heterogeneity index, Shannon's Diversity Index, measured for each study reach, as well as the percent area of in-stream structural elements. The results indicate two potential mechanisms for how relative sediment supply may drive geomorphic diversity in natural river systems at the reach scale. When less mobile structural elements form a small proportion of the reach landscape, the supply/capacity ratio dictates the range of sediment textures and geomorphic features observed within the reach. In these settings, channels with a moderate relative sediment supply exhibit the highest textural and geomorphic diversity. In contrast, when less mobile structural elements are abundant, forced local scour and deposition creates high habitat heterogeneity, even in the presence of high relative sediment supply.

Keywords: Bedload transport; Channel bed texture; Rivers; Aquatic habitat; Sediment mobility; Fluvial processes; Spatial heterogeneity; Landscape indices; Large woody debris

1. Introduction

Geomorphology and hydrology are the physical foundation of stream ecosystems. Channel morphology provides the structural basis of the aquatic environment, while discharge and hydraulic characteristics govern the volume and quality of the aquatic environment (Maddock, 1999). The interaction between hydrology, geomorphology, and aquatic species habitat across multiple spatiotemporal scales is often discussed in the literature, yet remains poorly understood (Imhof et al., 1996; Naiman et al., 1999; Petts, 2000). In particular,

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linking aquatic habitat characteristics to the physical processes that drive change within a watershed has been difficult (Imhof et al., 1996).

Riverine habitat heterogeneity–the inherent diversity of aquatic habitats throughout a stream environment–has become recognized as a key attribute of river ecosystems (Power, 1992). Studies have shown that greater heterogeneity in stream habitat increases aquatic species diversity (Beisel et al., 2000; Brown, 2003). Diversity in stream habitat provides not only a greater number of niches for species to occupy, but provides a greater variety of habitats available to species for breeding, foraging and refugia in the highly dynamic and variable environment of a river system (Townsend et al., 1997; Ward et al., 1999; Ward and Tockner, 2001). Despite the widespread recognition that habitat heterogeneity is important to aquatic ecosystems, few studies address the processes responsible for the creation and maintenance of heterogeneity.

At the reach scale, stream habitat heterogeneity and associated biological response are linked to physical processes that act at various spatial and temporal scales within a watershed (Poole, 2002). The balance between the sediment supply and transport capacity of a stream system is a fundamental driver of stream geomorphology (Pitlick and Wilcock, 2001), and dictates not only the aggradational or degradational state of a system, but controls channel morphology and substrate textures (Dietrich et al., 1989; Lisle et al., 1993)—two of the most important characteristics of physical habitat. At smaller scales, in-stream structural features, such as large woody debris and boulders, create local scour and deposition that contribute to increased habitat heterogeneity (Abbe and Montgomery, 1996; Buffington and Montgomery, 1999a). This study explores the complex interactions between riverine habitat heterogeneity and the geomorphic and hydraulic processes governing channel conditions by testing the hypothesis that maximum habitat heterogeneity occurs in stream reaches with a moderate relative local sediment supply, as measured by the sediment supply/transport capacity ratio. The influence of in-stream structural elements on both habitat heterogeneity and the supply/capacity ratio is also assessed to determine how local processes interact with relative sediment conditions and the quantitative measure of those conditions. Habitat heterogeneity is quantified using spatial heterogeneity measures from the field of landscape ecology (Li and Reynolds, 1995); relative sediment supply is quantified using a dimensionless bedload transport ratio, q^* (Dietrich et al., 1989).

2. Defining habitat heterogeneity and relative sediment supply

The processes creating physical habitat heterogeneity are often alluded to in the literature, but discussed only generally in qualitative terms that relate increased channel dynamics to increased channel complexity (e.g., Madej, 1999; McKenney, 2001). Studies have indicated that channel features increasing local scour and deposition, such as the presence of large woody debris, increase pool depth and frequency thereby increasing channel diversity (Ralph et al., 1994; Montgomery et al., 1995; Abbe and Montgomery, 1996). Similarly, changes in land use that result in bed degradation or loss of woody debris result in channel simplification (Horan et al., 2000; Buffington et al., 2002). Yet detailed studies that quantify heterogeneity and relate varying degrees of habitat heterogeneity to physical geomorphic and hydrologic processes are generally lacking.

Spatial aspects of morphological channel change are driven by discharge and sediment supply fluctuations, but modified by spatial feedbacks associated with internal channel morphology (Lane et al., 1996). Studies have shown that varying rates of sediment supply produce fundamentally different substrate textures (Buffington and Montgomery, 1999b; Lisle et al., 2000), while variations in both discharge and sediment supply control channel morphology (Dietrich et al., 1989; Lane et al., 1996; Massong and Montgomery, 2000). Stream reaches with a high relative sediment supply, where the volume of sediment overwhelms the capacity of the stream to transport the material, generally exhibit bed aggradation with unsorted, fine surface textures (Dietrich et al., 1989; Lisle et al., 1993), simple channel morphologies (Andrews, 1984; Madej, 1999), limited scour depth (Lisle, 1982; Buffington et al., 2002) and loss of usable habitat (Pitlick and Van Steeter, 1998).

Reaches with a low relative sediment supply, on the other hand, have the ability to transport most of the sediment supplied to the stream with little storage of sediment, leaving behind only the least mobile particles. The lack of sediment deposition creates bed degradation and results in simple featureless channels dominated by uniformly large coarse sediments. These conditions have been observed in flume studies at low sediment feed rates (Dietrich et al., 1989; Lisle et al., 1993) as well as in natural streams below dams (Power et al., 1996; Buffington and Montgomery, 1999a; Pitlick and Wilcock, 2001) and in high gradient mountain reaches where sediment deposition is associated only with debris flows (Benda and Cundy, 1990) and large woody debris (Montgomery et al., 1996).

Reaches with a moderate relative sediment supply therefore may exhibit the greatest geomorphic diversity by creating channel conditions with both variety in geomorphic features, such as scour pools and depositional bars, and a variety of surface textures from differential sorting of sediments at variable flows. This study attempts to address this question by testing the hypothesis that moderate relative sediment supply creates maximum spatial heterogeneity in morphology and surface texture (Fig. 1).

Multiple field studies have also shown, however, that internal channel structures, such as large woody debris and boulders, create local scour and deposition resulting in increased pool and bar frequency (Montgomery et al., 1995; Abbe and Montgomery, 1996). Reaches with a greater spatial extent of structures therefore may exhibit greater habitat heterogeneity. Furthermore, the interaction between in-stream structural features and relative sediment supply is not well understood. In reaches with a moderate or high relative sediment supply, deposition downstream of structural features may increase the local sediment supply providing sediment available for future mobilization; however, reaches with a low relative sediment supply may lack sediment for deposition regardless of the structures and therefore exhibit lower habitat heterogeneity. We hypothesize that the presence of in-stream structural features may act in conjunction with the relative sediment supply to increase habitat heterogeneity in all cases, but particularly when there is a moderate relative sediment supply.

To test these hypotheses, physical habitat heterogeneity was quantified using an ecologically meaningful spatial heterogeneity index, Shannon's Diversity Index (SHDI) (McGarigal and Marks, 1995). The term habitat heterogeneity is often used in the literature as a catch phrase to encompass a broad array of concepts ranging from spatial variation in flow to habitat patch richness. In this study, we define it specifically as the spatial complexity of geomorphic units within a stream reach. Although many spatial heterogeneity indices exist that quantify different aspects of physical habitat heterogeneity, SHDI was shown to be an ecologically meaningful metric for *Rana boylii* (Foothill Yellow-legged frog), a sensitive aquatic species occupying streams in the Sierra Nevada, California (Yarnell, 2005). In order to determine if relative sediment supply is correlated with varying degrees of habitat heterogeneity, use of a heterogeneity metric that is known to relate to biological patterns allows for not only indirect comparisons between physical and ecological patterns, but for an applied interpretation of potential relationships as well.

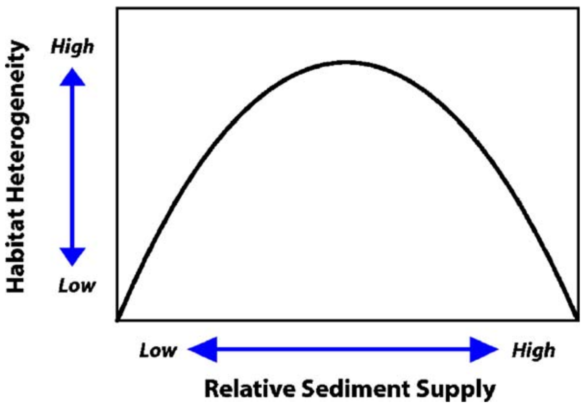

Fig. 1. Hypothesized theoretical relationship between physical habitat heterogeneity and relative sediment supply.

Relative sediment supply was quantified using a dimensionless bedload transport ratio, q^*—a metric based on hydraulic characteristics and surface texture that correlates with the amount of sediment supplied to the channel versus the ability of the stream to transport the sediment (Dietrich et al., 1989). This metric is useful not only for quantifying relative sediment supply in the field (Kinerson, 1990), but also for measuring sedimentation impacts on channel morphology and surface texture (Rutten, 1998; Lisle et al., 2000; Yarnell, 2000). The bedload transport ratio, q^*, is calculated from bedload transport equations that use field measured parameters as inputs:

$$q^* = \frac{q_s}{q_l} = \left(\frac{(\tau_b - \tau_{cs})}{(\tau_b - \tau_{cl})}\right)^{1.5} \tag{1}$$

where q_s is the sediment transport rate of the bed surface material, q_l is the sediment transport rate of the bedload, τ_b is the bed shear stress imposed by a flow, and τ_{cs} and τ_{cl} are the critical bed shear stresses required to initiate motion of the surface and bedload material, respectively. Field-measured parameters are used to calculate the shear stresses.

Other studies have found measures such as Shield's stress (τ^*) (Lisle et al., 2000) or competent median grain size (D'_{50}) (Buffington and Montgomery, 1999b) correlate with the sediment supply rate in gravel-bedded reaches. Uncertainties can arise in predicting the mean bedload transport rates used in calculating q^*, particularly due to high variability in local shear stress. As a result, calculations of q^* can be biased by the location of sediment samples taken within a reach. Reach-averaged values of Shield's stress and D'_{50} were shown to be somewhat less susceptible to local variation in shear stress and therefore in some streams to provide a good representation of the supply rate at the reach-scale. However, because these measures are derived primarily from the surface grain size distributions in a reach, comparisons between stream reaches with a wide range of mean surface grain sizes could affect calculated variations in each parameter. In addition, they are less directly linked to changes in sediment supply and thus less useful in predicting channel response (Lisle et al., 2000). Our interest in this study is focused specifically on how the relationship between sediment supply and transport capacity affects channel morphology; therefore, $q*$ is the most applicable metric to quantify the supply/capacity ratio provided care is taken in choosing sample locations and calculated results are verified where possible. Although not widely used in evaluations of stream habitat conditions specifically, $q*$ has been shown in a previous study to correlate with relative population densities of Foothill Yellow-legged frog (Yarnell, 2000), and therefore is also appropriate for comparisons between physical and ecological patterns.

3. Methods

The hypotheses were tested using data from two previously published flume studies, one previously published field study in the California Coast Range and a new field study on several tributaries to the South Yuba River in Nevada County, California, USA. In all cases, calculated supply/capacity ratio values and percent structural elements in each reach were plotted against SHDI measured for each study reach in order to assess the relationship between spatial habitat heterogeneity, spatial extent of structural elements and relative sediment supply.

SHDI was calculated for each study reach using the spatial analysis program FRAGSTATS v.3.3 (McGarigal et al., 2002). FRAGSTATS has been shown to be useful in analyzing categorical maps (Raines, 2002) and can directly evaluate raster-based grids exported from ArcGIS. The program includes a wide variety of metrics that can be calculated at three different scales of analysis: the patch-level, the class-level and the landscape-level. In this study, patches equate to individual habitat units, classes represent each habitat unit type (e.g., pool, riffle, bar, etc.) and the landscape is the study reach. SHDI was evaluated at the landscape level using the following equation:

$$\mathrm{SHDI} = -\sum_{i=1}^{m} (P_i^{*} \ln P_i) \tag{2}$$

where P_i is the areal proportion of the landscape occupied by habitat type i. SHDI increases as the number of different habitat types increases and/or the proportional distribution of area among patch types becomes more equitable (McGarigal and Marks, 1995). Habitat units were defined in the field following the definitions of Hawkins et al. (1993) and Wohl (2000). Additional details on how habitat units were measured and the use of SHDI as a measure of habitat heterogeneity can be found in Yarnell (2005). The spatial extent of structural elements in each reach, specifically large woody debris and boulders, was calculated as the percent area occupied within each reach. The 'percent structure' in each reach is the summation of the percent area of large woody debris and the percent area of boulder, where structural boulders are a minimum of 1 m^2 in planform view.

3.1. Previously published studies

Three previously published studies (two flume and one field) contained calculated $q*$ values and figures of the sediment texture and geomorphic characteristics of the study reaches. The two flume studies (Dietrich et al., 1989; Lisle et al., 1993) included figures depicting surface texture distributions from a series of flume runs where sediment supply was varied as discharge remained constant. For the current study, these figures were scanned; and each surface texture patch was delineated digitally in ArcGIS accounting for the location of specific features such as bars, pools and riffles where noted (Fig. 2). Once a planform map of each flume run was created, the data were input into FRAGSTATS for analysis. SHDI was calculated for each flume run and plotted against the published $q*$ values. Because structural elements were not present in either of the flume runs, percent structure was not calculated in FRAGSTATS.

The methods for calculating $q*$ for each flume study varied slightly because of the choice of bed shear stress equations used in the $q*$ equation. Both studies incorporated the Shield's shear stress relation to calculate the critical shear stress required to initiate particle movement (Eq. (3)); however, Dietrich et al. (1989) calculated boundary shear stress using flow depth and the energy slope (Eq. (4)), while Lisle et al. (1993) computed boundary shear stress from mean variables for the channel as a whole, specifically incorporating both barform and grain resistances (Eq. (5)):

$$\tau_c = \tau_{*c} g(\rho_s - \rho)(D_{50}) \tag{3}$$

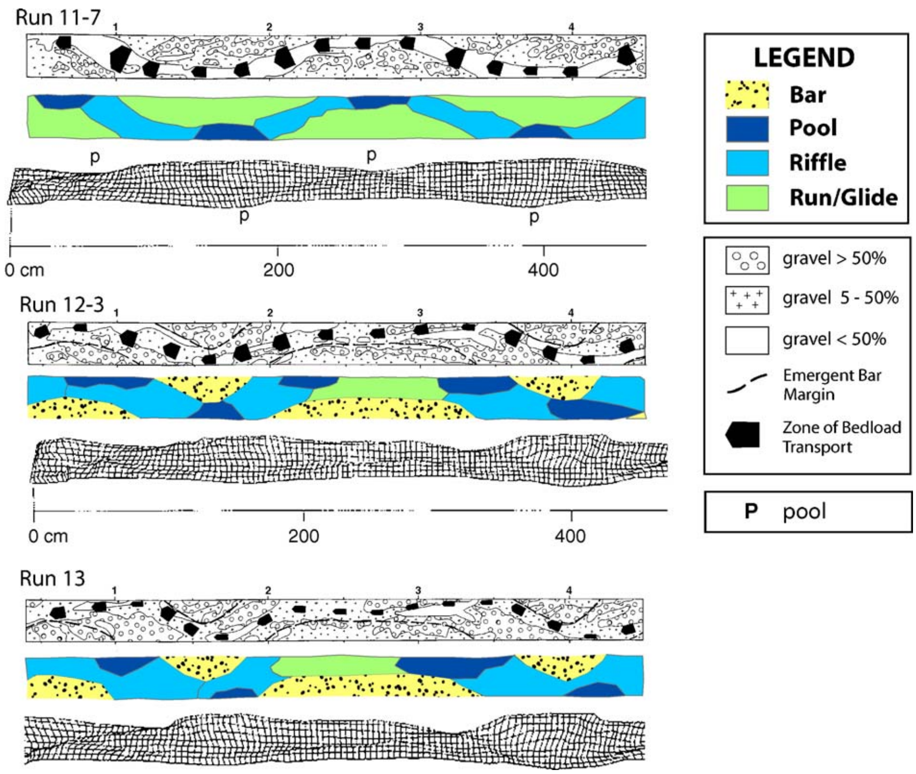

Fig. 2. Scanned maps of sediment distribution in flume (Lisle et al., 1993) and corresponding digitized planform map input to FRAGSTATS for analysis. Flume runs 11-7 (high relative supply), 12-3 (moderate relative supply) and 13 (low relative supply) are depicted. The top figure for each run shows a planform view of the bed surface facies in the flume; immediately below is the corresponding digitized map of geomorphic units input to FRASTATS; the bottom figure for each run shows an oblique topographic view of the channel surface delineating bars and pools.

where τ_c is the critical bed shear stress, τ_{*c} is the empirically derived Shield's constant, $g(\rho_s - \rho)$ is the submerged specific gravity of sediment and D_{50} is the median particle size of the bedload or surface material as applicable;

$$\tau_b = \rho g h s \tag{4}$$

where τ_b is the bed shear stress, ρ is the density of water, g is gravity, h is the depth of water and s is the water surface slope; and

$$Q^* = \left(\frac{(\tau_G + \tau_B) - \tau_{cs}}{(\tau_G + \tau_B) - \tau_{cl}} \right)^{1.5} \tag{5}$$

where Q^* is used in place of q^* to denote a value that is computed from mean variables from the channel as a whole, τ_B is the shear stress related to bar resistance, τ_G is the shear stress related to grain resistance, and τ_{cl} and τ_{cs} are the critical shear stress of the bedload and surface material, respectively.

The addition of bar resistance in the Lisle et al. (1993) calculations may explain the variability in range of values between the two studies. Q^* values calculated at high sediment feed rates in the Lisle et al. (1993) study were postulated to have been lower than expected because of the coarseness of bar heads where large particles accumulated as the bars were formed. Increased grain diameter in the local surface material would result in a lower average Q^* value. However, within each flume study, the q^* and Q^* values quantified low, moderate and high relative sediment supplies.

The field study by Kinerson (1990) was evaluated in a similar fashion to the flume studies. Maps of each study reach were scanned, digitized in ArcGIS to delineate varying surface textures and geomorphic features, and input into FRAGSTATS to determine SHDI and percent structure (Fig. 3). Although Kinerson (1990) calculated q^* using the same sediment transport equation as Dietrich et al. (1989), several assumptions were made to account for complexities inherent to natural field conditions. Unlike the flume studies where the controlled environment allowed for exact measurements of the bedload supply material, the grain size distribution of the bedload could not be obtained

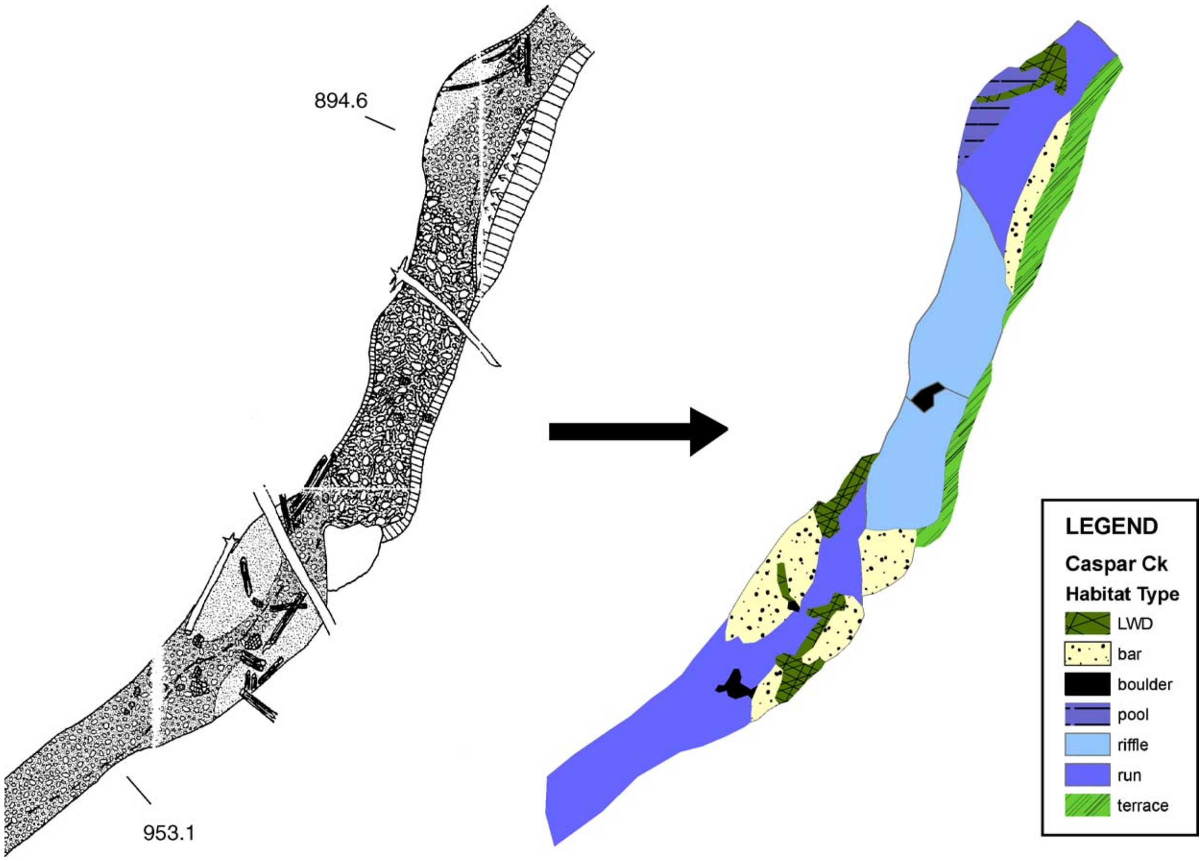

Fig. 3. Field map of Caspar Creek study reach (Kinerson, 1990) and corresponding digitized planform map input to FRAGSTATS for analysis.

directly in the field. As a result, the subsurface material was used as a proxy for the bedload material. Similarly, use of Eq. (3) to calculate the bed shear stress is a rough approximation of actual shear stresses occurring in a natural stream. It is only applicable in channels with simple geometry where grain roughness dominates over bedform roughness and where there is uniform steady flow, at least locally. Therefore, to account for wide variations in surface texture and local shear stresses, Kinerson (1990) calculated several local q^* values throughout each field study reach to reflect local conditions. These local q^* values were then qualitatively compared with visual assessments of the relative sediment supply within each study reach. Similar to conclusions from the flume studies, Kinerson (1990) concluded that the quantitative q^* values adequately depicted low, moderate and high relative sediment supplies.

For this study, in order to compare the q^* (Q^*) values from the flume studies (which quantify relative sediment supply throughout the flume at a reach scale) with the multiple local q^* values in the field study (which quantify relative sediment supply at a subreach scale), we averaged the local q^* values within each field study reach to obtain a $\overline{q^*}$ value reflecting overall relative sediment supply in the reach. The reach-averaged $\overline{q^*}$ values calculated from the Kinerson (1990) data consistently reflect the qualitative sediment supply for each study reach as determined in the original field study.

3.2. South Yuba River field study

Eight study reaches were selected across four tributaries to the South and Middle Yuba Rivers ranging from low to high relative sediment supplies (Fig. 4, Table 1). The four study creeks are similar to most mid-elevation drainages in the Sierra Nevada mountain range in California having moderate to steep slopes, confined valleys with occasional bedrock outcrops, narrow disconnected riparian zones, coarse substrates and steep channel morphologies including

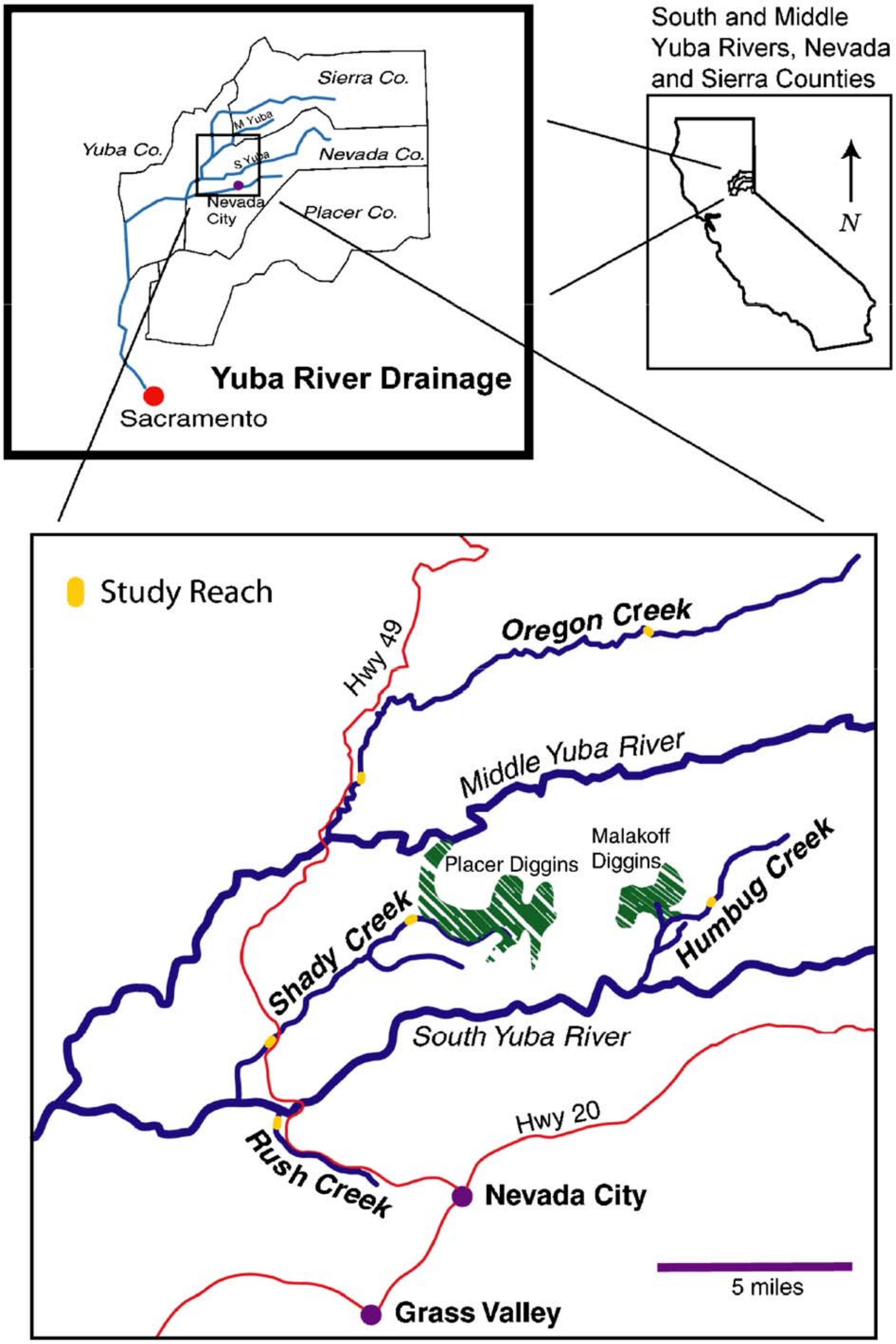

Fig. 4. Location of study reaches in tributaries to South and Middle Yuba Rivers, California. Placer and Malakoff Diggins are open hydraulic mine pits that contribute sediment to Shady and Humbug Creeks, respectively.

cascades, steps, riffles and pools. All four creeks have been subject to various land uses, including mining (in-stream, hydraulic and high banking), logging and development, but the degree of impact varies between each creek resulting in varied habitat complexity between and within each watershed. Shady Creek differs from the other study creeks in that it continues to recover from extensive past aggradation of hydraulic mining debris. Some Shady Creek reaches with steeper slopes have recovered to the original bedrock

Table 1
Geomorphic characteristics of study reaches

Creek	Study reach	Reach type	Reach length (m)	Drainage area upstream (km^2)	Estimated mean annual discharge (cfs)	Dominant geomorphic features	Dominant substrate size	Relative sediment supply
Shady	Dead Tree Scape	Braided	92	1.7	2	Low gradient riffles, many fine/coarse bars, shallow pools	Gravel	High
Shady	Rust Pit	Plane bed	81	14.0	6	Low gradient riffles, few fine/coarse bars	Gravel	Low
Shady	Shady Road	Riffle-pool	97	22.7	9	Low gradient riffles, shallow pools, coarse bars	Gravel	Moderate
Rush	Aaron's Pools	Step-pool	57	14.6	10	Boulder steps, plunge pools, coarse bars	Cobble	Moderate
Rush	Road Jumble	Cascade	80	14.6	10	Boulders, coarse bars, high gradient rapids	Boulder	Low
Oregon	Celestial Pools	Step-pool	88	85.4	33	Boulder steps, plunge pools	Boulder	Moderate
Oregon	Oregon Creek Road	Cascade	65	27.7	11	Boulders, coarse bars, high gradient rapids	Boulder, cobble	High
Humbug	Blair Pond	Step-pool	58	10.4	7	Boulder steps, plunge pools, coarse bar	Boulder, cobble	Moderate

surfaces, but the majority of reaches continue to degrade through vast piles of tailings leaving remnant terraces behind. Across watersheds, Shady Creek has the highest relative sediment supply, followed by Oregon, Humbug and Rush Creeks, respectively.

The study reaches were chosen as representative of geomorphic conditions common to each creek and to reflect a range in relative sediment supply within each watershed. Following the methods of Kinerson (1990), qualitative designations of relative sediment supply for each study reach were made based on observations of depositional features (such as bars, deposits on the downstream side of boulders and fine patches) and erosional features (such as exposed cutbanks, scour and lack of fines). In addition, hillsides, banks and tributaries were examined for evidence of direct sediment input. As a result, the qualitative designation of relative sediment supply (high, moderate or low) for each study reach reflects the degree of sedimentation in that study reach in comparison to other reaches within that watershed (Table 1). Given the potential bias in $q*$ due to sediment sample location, this qualitative evaluation was used as an independent assessment of relative sediment supply to verify the calculated reach-averaged $\overline{q*}$ values.

The geomorphic features in each reach were surveyed directly with a total station and input into ArcGIS to create detailed planform maps similar to that depicted in Fig. 2 that could be imported into FRAGSTATS for analysis. Detailed methods of the field mapping, ArcGIS conversion and FRAGSTATS analysis are described in Yarnell (2005). As with the analysis of the Kinerson (1990) field study, both SHDI and the percent area of each geomorphic feature and structural element were calculated using FRAGSTATS for comparison with field-determined $\overline{q*}$ values.

The relative sediment supply for each study reach was determined using methods described by Kinerson (1990). Eq. (1) was used to calculate $q*$ and critical shear stress values were based on grain roughness using the Shield's stress relation (Eq. (2)). Channel bed slope, bankfull depth and surface and subsurface grain size distributions were measured in the field and used to calculate Eqs. (3) and (4) (Table 2). Surface grain size distributions were determined from Wolman pebble counts (Wolman, 1954), and subsurface grain size distributions were calculated from field-sieved bulk samples (Harrelson et al., 1994). Sediment samples within each study reach were taken where sediment deposition was least influenced by local in-stream structures: at the top center of bankfull height bars, the center and bankfull edge of riffles, and the thalweg location in plane bed reaches. Depositional features associated with in-stream structures (such as lee side deposition bars, sediment pockets behind boulders or scour pools) were avoided. Bankfull depth was determined from hydraulic geometry relations calculated from field measurements of cross-sectional area, discharge and velocity. Where possible, the bankfull

Table 2
Summary of $q*$ calculations. Channel slope, surface and subsurface grain sizes, and bankfull height are field measured values

Site	Channel slope	Surface D_{50} (mm)	Subsurface D_{50} (mm)	Paving ratio	Bankfull height (m)	Bankfull bed shear stress (surface) (N/m^2)	Critical bed shear stress (surface) (N/m^2)	Ratio of bankfull to critical shear stresses	Critical bed shear stress (subsurface) (N/m^2)	$q*$ value
Dead Tree Scape	0.013	22.3	13.0	1.71	0.18	23.46	16.19	1.45	9.46	0.37
Rust Pit	0.015	23.7	7.4	3.20	0.16	23.03	17.25	1.34	5.38	0.17
Shady Road	0.013	31.0	8.0	3.88	0.25	31.43	22.58	1.39	5.82	0.28
Aaron's Pools	0.035	104.7	14.4	7.27	0.26	89.18	50.79	1.76	6.99	0.27
Road Jumble	0.040	93.0	13.9	6.69	0.22	84.93	45.11	1.88	6.74	0.36
Celestial Pools	0.031	101.6	18.0	5.65	0.42	127.60	73.95	1.73	13.10	0.36
Oregon Creek Road	0.029	53.9	10.6	5.08	0.31	88.10	39.20	2.25	7.71	0.49
Blair Pond	0.033	76.0	18.0	4.22	0.25	80.85	36.85	2.19	8.73	0.50

depth was verified in the field with measurements of standard bankfull indicators (Harrelson et al., 1994).

Bedload measurements obtained during high flows on Shady Creek were used to verify Eq. (1) as a reasonable estimate of observed bedload transport and to calculate a Shield's constant that was appropriate for the specific channel conditions. For all bedload samples taken, the bedload grain size distribution was similar to the reach-averaged grain size distribution of the subsurface. The Shield's constant was calculated to be 0.045 at bankfull flow on two of the Shady Creek study reaches. This value was used in Eq. (2) for each of the Shady Creek study reaches. During the study period (Water Year 2001–2002), winter flows were not high enough to initiate bedload transport on the remaining three study creeks. Therefore, a Shield's number of 0.03 was used to estimate initial motion reflecting the coarser, more stable nature of the remaining study reaches (Andrews, 1983, Lisle et al., 2000). Local calculations of $q*$ from a variety of subreach locations (such as the thalweg, bars, riffles and bankfull edges) were averaged throughout each study reach to obtain a $\overline{q*}$ value representing the dimensionless bedload transport ratio of the channel as a whole. Because of high variability in local shear stress associated with in-stream structures, sediment samples were not taken immediately adjacent to in-stream structures or from any feature obviously associated with an in-stream structure (e.g. base of a pool or lee-side sediment pocket). Lastly, the calculated $\overline{q*}$ values were compared to qualitative observations of the relative sediment supply in each reach to verify the assumption that observed surface textures reflected the degree of relative sediment supply.

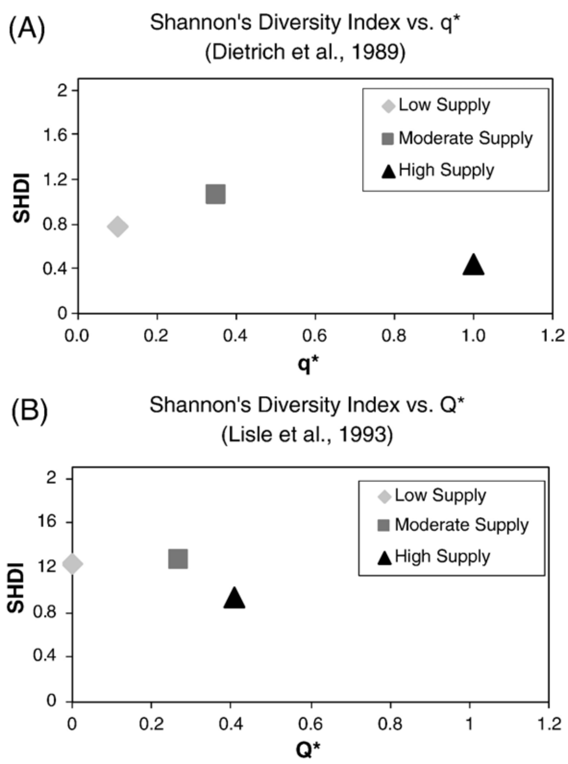

Fig. 5. Relationship between relative sediment supply ($q*$ or $Q*$) and geomorphic diversity (SHDI) for (A) Dietrich et al. (1989) flume study and (B) Lisle et al. (1993) flume study.

4. Results

Within each of the flume studies, the flume run with the moderate relative sediment supply had the highest SHDI value (Fig. 5, Table 3). Data from the two field studies, however, showed a linearly increasing trend such that as relative sediment supply increased, SHDI increased (Fig. 6).

The primary geomorphic difference between the field and flume conditions was the presence in the field study reaches of less mobile structural elements, such as large woody debris and boulders. To determine if geomorphic diversity was related to the presence of the structural elements, SHDI was plotted against the percent area of large woody debris and boulders (Fig. 7). For both field studies, SHDI linearly increased as the percent structure within the study reach increased.

Because SHDI was positively correlated with both the $\overline{q^*}$ values and the percent area of structural elements, $\overline{q^*}$ was plotted against the percent structural elements for each field study reach (Fig. 8). Although a clear trend to the data was not apparent, $\overline{q^*}$ was generally high when the percent structure was > ∼ 2% of the total area. In reaches where the percent structure was low, a full range of $\overline{q^*}$ values occurred. To further examine the relationship between $\overline{q^*}$ and percent structure, a regression analysis was completed on the Yuba Rivers study data in SPSS v.12 (2003). Various parameters that comprise $\overline{q^*}$, specifically, the four field-measured parameters (slope, bankfull depth, surface D_{50} and subsurface D_{50}) and the ratio between bankfull and critical shear stress (τ_b/τ_c) were compared with the percent structure. Three of the four field-measured parameters were highly correlated with the percent structure (Table 4), indicating that reaches with higher slopes and larger grain sizes have greater spatial extents of in-stream structure. In the Yuba River tributaries, higher slope reaches have a greater volume input of large woody debris and boulders from the steep hillside banks. The ratio between bankfull and critical shear stress (τ_b/τ_c) (which was linearly correlated with $\overline{q^*}$ (R_2=0.72, p=0.008)) was not well correlated with percent structure, although it was generally higher in reaches with greater percent structure. These results indicate that, while $\overline{q^*}$ was qualitatively verified to reflect relative sediment supply, the influence of higher slope and greater surface grain size on the calculation of $\overline{q^*}$ creates uncertainty in whether $\overline{q^*}$ is reflecting processes

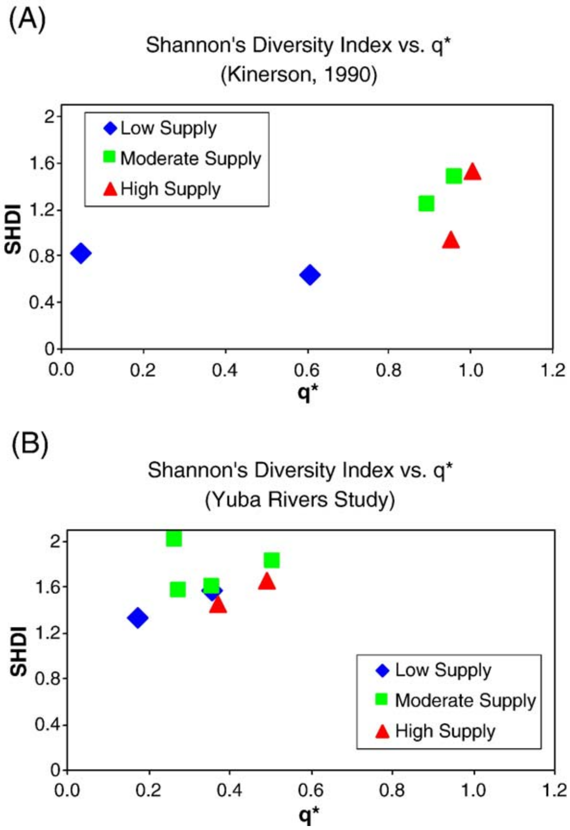

Fig. 6. Relationship between relative sediment supply ($\overline{q^*}$) and geomorphic diversity (SHDI) for (A) Kinerson (1990) field study and (B) Yuba Rivers field study.

Table 3
Summary of calculated q^* (Q^*) values and Shannon's Diversity Index values for each study

Study	Site/reach	Relative supply	q^* or Q^*	SHDI
Dietrich et al. (1989)	Flume	Low	0.10	0.77
	Flume	Moderate	0.35	1.06
	Flume	High	1.00	0.44
Lisle et al. (1993)	Flume	Low	0.00	1.23
	Flume	Moderate	0.27	1.27
	Flume	High	0.41	0.93
Kinerson (1990)	Lagunitas	Low	0.05	0.82
	Sagehen	Low	0.61	0.64
	Caspar	Moderate	0.96	1.49
	Jacoby	Moderate	0.89	1.24
	Prairie	High	0.95	0.94
	Wildcat	High	1.01	1.53
South Yuba River	Dead Tree Scape	High	0.37	1.46
	Rust Pit	Low	0.17	1.33
	Shady Road	Moderate	0.28	1.57
	Aaron's Pools	Moderate	0.27	2.02
	Road Jumble	Low	0.36	1.57
	Celestial Pools	Moderate	0.36	1.61
	Oregon Creek Road	High	0.49	1.66
	Blair Pond	Moderate	0.50	1.83

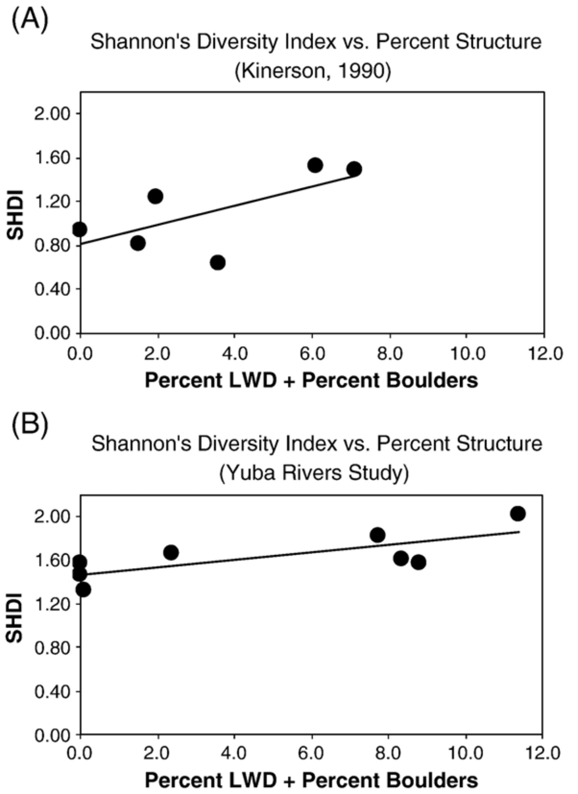

Fig. 7. Plot of Shannon's Diversity Index vs. percent area of structural elements for (A) Kinerson (1990) field study (R^2=0.52, F=4.32, p=0.11) and (B) Yuba Rivers field study (R^2=0.54, F=7.16, p=0.04).

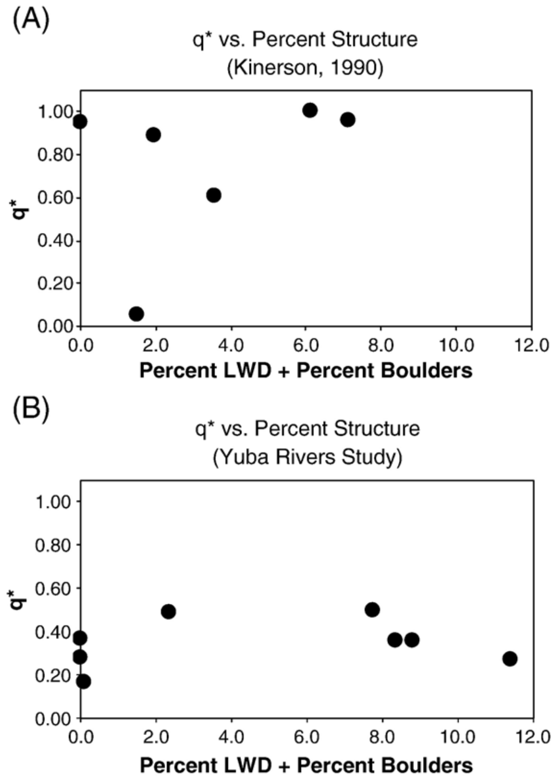

Fig. 8. Relationship between reach-averaged $\overline{q*}$ and percent area of structural elements for (A) Kinerson (1990) field study and (B) Yuba Rivers field study.

driven by larger scale sediment supply or more local processes influenced by the greater degree of structure.

In order to examine the relationship between SHDI and $\overline{q*}$ without the overriding influence of a high degree of structural elements, only those field reaches with a low percentage of large woody debris and boulders were plotted (Fig. 9). Without the presence of less mobile elements, those reaches with moderate relative sediment supplies and moderate values of $\overline{q*}$ had the highest SHDI values, similar to the results observed in each of the flume studies.

The data from all four studies, excluding those field reaches where structural elements comprised > ~ 2% of the total reach area, were examined categorically as a way to compare the results across studies with different methodologies. A plot of SHDI against categories of high, moderate and low relative sediment supply showed a broad unimodal trend for each study as well as for the average SHDI among all studies (Fig. 10). These results suggest reaches with a moderate relative sediment supply as measured by the supply/capacity ratio had the highest geomorphic diversity as measured by SHDI.

5. Discussion

Of the many physical and ecological processes that contribute to the creation and maintenance of in-stream aquatic habitat, one of the more difficult relationships to demonstrate is the linkage between geomorphic habitat heterogeneity and sediment transport characteristics (Imhof et al., 1996). In particular, quantification of the relationship between sediment supply and transport capacity, in a manner that is easily and clearly

Table 4
Results from linear regression of each field measured parameter input to $q*$ with percent structure

Parameter	R^2	p-value
Slope	0.82	0.002
Surface D_{50}	0.95	<0.001
Subsurface D_{50}	0.58	0.028
Bankfull depth	0.19	0.283

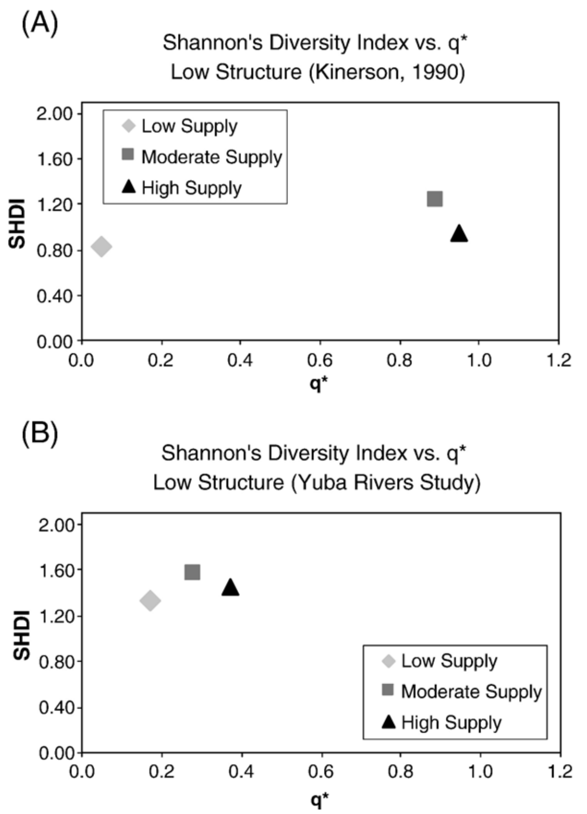

Fig. 9. Relationship between relative sediment supply ($\overline{q^*}$) and geomorphic diversity (SHDI) in reaches with <2% structural elements for (A) Kinerson (1990) field study and (B) Yuba Rivers field study.

accomplished in the field, remains a fundamental research challenge. However, the findings of this paper–consistent across the flume and field studies–suggest a discernable relationship exists between relative sediment supply and habitat heterogeneity that warrants further investigation.

Although $\overline{q^*}$ provided a good quantification of relative sediment supply in the Yuba Rivers field study when verified by an independent qualitative analysis, a clear relationship between $\overline{q^*}$ and SHDI in field reaches with high degrees of structure could not be determined from these results. The high correlation of the field measured parameters (slope, sediment size and bankfull depth) with the percent structure creates uncertainty when evaluating the relationship between $\overline{q^*}$ and SHDI, which is also highly correlated with percent structure. The relationship between the supply/capacity ratio and SHDI can only be evaluated with confidence in the flume study data and the field data where percent structure is very low or insignificant. While these data are limited, only 3 data points for each study, the consistency of the trend across each study (Fig. 10) suggests relative sediment supply may be a driving factor in the degree of habitat heterogeneity in a reach.

The results, given that $\overline{q^*}$ and SHDI are related as discussed above, suggest two potential mechanisms for how relative sediment supply may be driving geomorphic diversity in natural river systems at the reach scale. When less mobile structural elements, such as large woody debris and boulders, are not a significant proportion of the reach landscape, the relationship between sediment supply and transport capacity appears to dictate the range of sediment textures and geomorphic features observed within the reach. A moderate relative sediment supply creates channel conditions where differential scour and deposition result in pools, riffles and bars, each with varying sorted surface textures. These features are mobilized, scoured and deposited at different temporal and spatial scales depending on variability in the flow regime. Unlike channels with high relative sediment supplies

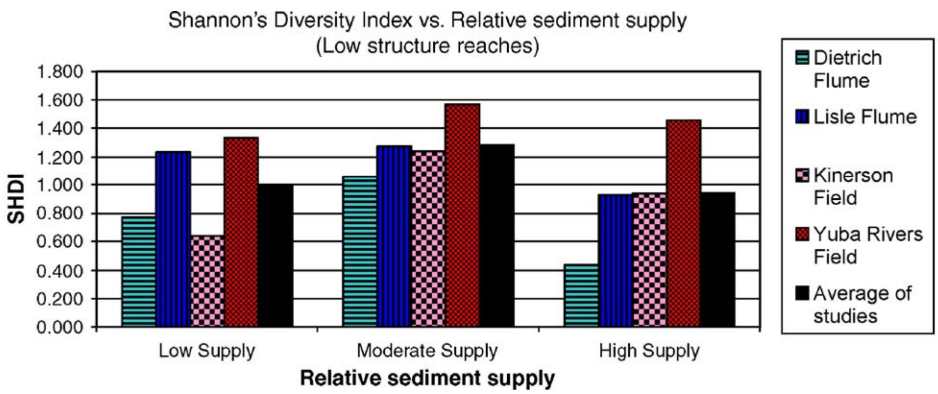

Fig. 10. Plot of relative sediment supply (categorical) vs. geomorphic diversity (SHDI) for reaches from all four studies where percent area of structural elements was <2%.

where the bed material is continually in motion and highly unsorted, or reaches with low relative sediment supplies where the substrate rarely mobilizes, channels with a moderate relative sediment supply may exhibit a relatively high diversity of geomorphic features, a relatively high diversity of surface textures, and thus a high overall heterogeneity in physical habitat types available at any given flow.

In contrast, when boulders and large woody debris become an increasingly larger proportion of a channel reach, habitat heterogeneity is likely “forced” by interactions among the less mobile structural elements, flow and bedload. The structural elements constrict and alter local flow paths, creating greater variations in local flow velocities. As the structure diverts flow, higher velocities are forced to the outer edges of the structure promoting local scour. The scoured sediments are often deposited just downstream as velocities decrease in the wake of the structure (Buffington and Montgomery, 1999a; Manga and Kirchner, 2000). As a result, the relative sediment supply is locally increased from the scour and deposition, creating a greater variety of geomorphic features and sorted sediment textures, and thereby increasing the heterogeneity in physical habitat types.

The data indicate that, regardless of the mechanism, processes that increase differential scour and deposition create an increased variety of geomorphic features and surface textures, resulting in greater physical habitat diversity. These processes may either be related to the relationship between transport capacity and sediment supply as hypothesized or to local hydraulic processes influenced by less mobile structural elements such as large woody debris and boulders. The study results indicate both mechanisms may occur, with the influence of structural elements overriding the relative sediment supply once some threshold is passed (e.g., when structural elements comprise $> \sim 2\%$ of the total reach landscape as observed in this study).

As a logical extension of these results, we suggest physical habitat complexity is likely maximized through a combination of a locally moderate sediment supply and a varied flow regime. The interaction of moderate sediment influx with variable flow magnitude and frequency creates the variations in sediment mobility required to maximize geomorphic diversity. In stream reaches where sediment supply is low, such as downstream of dams, high flow variability may have little impact on stream geomorphology as there is no sediment to sort and redistribute. In these types of reaches, a higher percentage of structural elements may promote deposition of what little sediment moves through the system thereby slightly increasing geomorphic diversity, but overall geomorphic heterogeneity will remain limited. In streams with high sediment supply but low flow variability, geomorphic diversity will also be low as the hydraulic processes required to sort sediment are limited. Unlike low sediment supply reaches, however, high supply reaches may exhibit increased diversity with a more varied flow regime. An increase in flow variability would promote differential sediment mobility increasing textural sorting, in essence transitioning a reach with high relative sediment supply to a moderate relative sediment supply. In this case, an increased percentage of structural elements would further encourage local scour and deposition resulting in a greater overall geomorphic diversity. The resulting conclusion is that, while increased structural elements do promote greater habitat heterogeneity in many instances, maximum geomorphic diversity is likely achieved when sediment supply relative to transport capacity is moderate and the flow regime is varied.

6. Conclusions

Using data from three previously published studies and a new field study conducted in the northern Sierra Nevada range, California, this study examined the interactions between relative sediment supply, habitat heterogeneity and in-stream structural elements. Results indicate that spatial and textural complexity in gravel-bedded streams reaches a maximum in reaches with intermediate relative supply values. However, this observation applies principally to streams with low abundances of less mobile in-stream structures, such as boulders and large woody debris. Habitat heterogeneity is positively correlated with the abundance of in-stream structures, even when relative sediment supply is high. These results indicate two potential mechanisms for creation and maintenance of habitat heterogeneity in alluvial stream reaches. When structural elements are minimal or lacking, the relationship between the sediment supply and the transport capacity drives the range of geomorphic features and sediment textures observed. Reaches with a moderate relative sediment supply have enough sediment to promote deposition and textural sorting, but are not so inundated with sediment that scour features are filled with fines; the result is a channel with high habitat heterogeneity. Conversely, when large woody debris and other less mobile structural elements dominate the channel, local scour and erosion force deposition and textural sorting downstream of the structures and result in increased habitat diversity.

These results support the generally accepted notion that additions of large woody debris to a stream channel increase habitat heterogeneity (Abbe and Montgomery, 1996; Buffington and Montgomery, 1999a). However, in order to maximize geomorphic diversity in a stream reach, both the degree of relative sediment supply and variability in flow must be considered. Additions of structural elements to channels in an effort to increase habitat diversity may have little impact in reaches with a low sediment supply. In these reaches, techniques designed to increase local sediment supplies, such as gravel augmentation or increasing access to sediment stored in banks, may have a larger effect. If a stream reach has been severely impacted by excess sediment on the other hand, introduction of structural elements to promote local scour and deposition may increase geomorphic diversity along with techniques designed to reduce sediment inputs to the channel.

For aquatic species known to respond directly to geomorphic conditions in a stream reach, such as salmonids, river-dwelling amphibians and benthic macroinvertebrates, additional insight into how habitat diversity is created and maintained is beneficial for conservation efforts. High gradient streams where these aquatic species often reside generally exhibit physical conditions indicative of moderate to low relative sediment supplies (Montgomery and Buffington, 1997). Boulder substrates, limited depositional features and lack of scour pools may limit habitat suitability. Increased sediment inputs are likely to offset these limitations in high gradient reaches, producing greater habitat diversity. For example, reaches near tributary confluences where debris inputs are high and flow is more variable have been suggested to be “biodiversity hotspots” because of high habitat heterogeneity (Benda et al., 2003, 2004). This heterogeneity stems from variable inputs of large woody debris and coarse sediment from the tributary into the main stem. These inputs create locally high sediment supply in an otherwise supply-limited reach and increase local scour and deposition. Similarly, wide valley segments have a greater potential for large woody debris input from floodplains and coarse sediment input from terraces and banks. The resulting increase in local scour and deposition from these inputs may also create greater geomorphic diversity within localized stream reaches. Conservation and restoration efforts should therefore focus on these areas where natural processes act to create and sustain local habitat diversity.

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