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Macroinvertebrate Community Responses to Gravel Addition in a Southeastern Regulated River

Ryan A. McManamay[1,*], Donald J. Orth[2], and Charles A. Dolloff[3]

Abstract - Sediment transport, one of the key processes of river systems, is altered or stopped by dams, leaving lower river reaches barren of sand and gravel, both of which are essential habitat for fish and macroinvertebrates. One way to compensate for losses in sediment is to supplement gravel to river reaches below impoundments. Because gravel addition has become a widespread practice, it is essential to evaluate the biotic response to restoration projects in order to improve the efficacy of future applications. The purpose of our study was to evaluate the response of the macroinvertebrate community to gravel addition in a high-gradient, regulated river in western North Carolina. We collected benthic macroinvertebrate samples from gravel-enhanced areas and unenhanced areas for 1 season before gravel addition, and for 4 seasons afterwards. Repeated measures multivariate analysis of variance indicated that the responses of macroinvertebrates to gravel addition were generally specific to individual taxa or particular functional feeding groups and did not lead to consistent patterns in overall family richness, diversity, density, or evenness. Non-metric multi-dimensional scaling showed that shifts in macroinvertebrate community composition were temporary and dependent upon site conditions and season. Correlations between macroinvertebrate response variables and substrate microhabitat variables existed with or without the inclusion of data from enhanced areas, which suggests that substrate-biotic relationships were present before gravel addition. A review of the current literature suggests that the responses of benthic macroinvertebrates to substrate restoration are inconsistent and dependent upon site conditions and the degree habitat improvement of pre-restoration site conditions.

Introduction

One of the primary functions of river systems is the transport of abiotic and biotic materials from upstream sources (Kondolf 1997, Vannote et al. 1980), which is governed by a stream's natural flow regime (Poff et al. 1997). The flow regime, in conjunction with associated physical and chemical processes, forms the habitat template for the occupation by species at various life stages (Poff et al. 1997, Trush et al. 2000, Vannote et al. 1980). Sediment transport, one of the key processes in river systems, maintains channel morphology and provides spawning and refuge habitats for many fish and macroinvertebrates (Trush et al. 2000).

According to Vitousek et al. (1997), more freshwater systems have been altered than any other ecosystem, with only two unimpounded rivers in the US; two thirds of the world's rivers are regulated. Following dam construction, the movement of material typically transported by a river system is altered, if not

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stopped, and the material settles out within the impoundment (Kondolf 1997). If sediment supply from upstream reaches does not equal the river's capacity to carry sediment downstream, then downstream areas are degraded by the removal of materials from the riverbed, the riverbed becomes coarsened, and the channel reaches a new state of equilibrium (Gordon et al. 2004, Kondolf 1997). The channel's morphology may take centuries to reach equilibrium, or it might never do so (Poff et al. 1997). In order to restore morphological processes, gravel and sediment can be supplemented to river reaches below impoundments to compensate for losses in sediment transport (Kondolf 1997).

Gravel additions have become an increasingly common tool used to enhance salmonid spawning habitats in dammed western gravel-bed rivers (Bunte 2004, Kondolf et al. 1996, Merz and Chan 2005, Merz and Setka 2004). Widespread declines in many Pacific salmon stocks, 54% of which are listed as endangered or threatened (NOAA 2012), have resulted in intensive restoration efforts (Katz et al. 2007). Multiple studies have assessed invertebrate responses to gravel addition, primarily due to the importance of these organisms as salmonid food (Merz and Chan 2005, Watry and Merz 2009). Gravel addition has been used successfully to enhance salmon spawning habitat (Kondolf et al. 1996, Merz and Setka 2004). The results from studies assessing invertebrate responses to gravel addition, however, are equivocal (Albertson et al. 2010, Merz and Chan 2005, Sarriquet et al. 2007, Watry and Merz 2009).

Gravel additions below dams in the eastern US have been used less frequently. We found two documented gravel-addition projects in Southeastern tailwaters in Georgia, which were undertaken to improve spawning habitats for *Moxostoma robustum* Cope (Robust Redhorse), a state-listed endangered species and a candidate for federal listing (SARP 2008a, 2008b). Typically, gravel augmentation has been conducted in alluvial channels. Little to no information exists, however, about gravel addition projects in high-gradient, non-alluvial channels and the biotic response to habitat enhancement (McManamay et al. 2010).

The Cheoah River is a regulated, high-gradient, non-alluvial system in western North Carolina. The construction of the Santeetlah Dam in 1927 trapped all bedload and prevented most sediment from entering the lower river, and moderate-to-high flood-flows were reduced. As a result, the streambed below the dam lacks the gravel substrate important as a refuge for macroinvertebrates, including one endangered mussel, and as spawning habitat for fish. To remediate degraded habitats, a Federal Energy Regulatory Commission (FERC) order established a gravel enhancement plan, which required the addition of washed aquatic gravel to the Cheoah River starting in 2008, and biological monitoring to inform adaptive adjustments to the program (FERC 2006). Given the short timeframe, assessing the biological responses of the macroinvertebrate community seemed to be the most realistic and tangible short-term study approach to detect habitat enhancement effects (Miller and Hobbs 2007). In addition, our study provides baseline data for long-term biomonitoring of the Cheoah River, which is a priority conservation watershed identified by the North Carolina Wildlife Resources Commission (NCWRC 2012). Prior to this study, the most recent benthic macroinvertebrate community sampling in the Cheoah River occurred in 2000 (Fig. 1; i.e., Pennington and Associates 2001). Our study, therefore, provides an initial assessment of macroinvertebrates after the new FERC license conditions were imposed. The purpose of this study is to provide an example of how gravel addition influences the macroinvertebrate community and physical habitat conditions of the streambed in a high-gradient, sediment-starved system in the eastern US.

Methods

Study site

The Cheoah River is a high-gradient (≈1.3%) regulated system located in western North Carolina within the Blue Ridge physiographic province (Fig. 1). The Cheoah River drains Santeetlah Lake, a 456-km^2 reservoir, and the river runs 14.6 km before emptying into the Little Tennessee River System. The watershed is predominately forested, has steep-valley relief (30% average slope), and is located within Nantahala National Forest (McManamay et al. 2010).

Because the dam releases water from the reservoir surface, sediment supply has been cut-off from entering the Cheoah River and is limited to input from tributaries and episodic landslides below Santeetlah Dam (Dilts et al. 2003, Normandeau Associates 2002). Before 2005, the flow within the Cheoah River

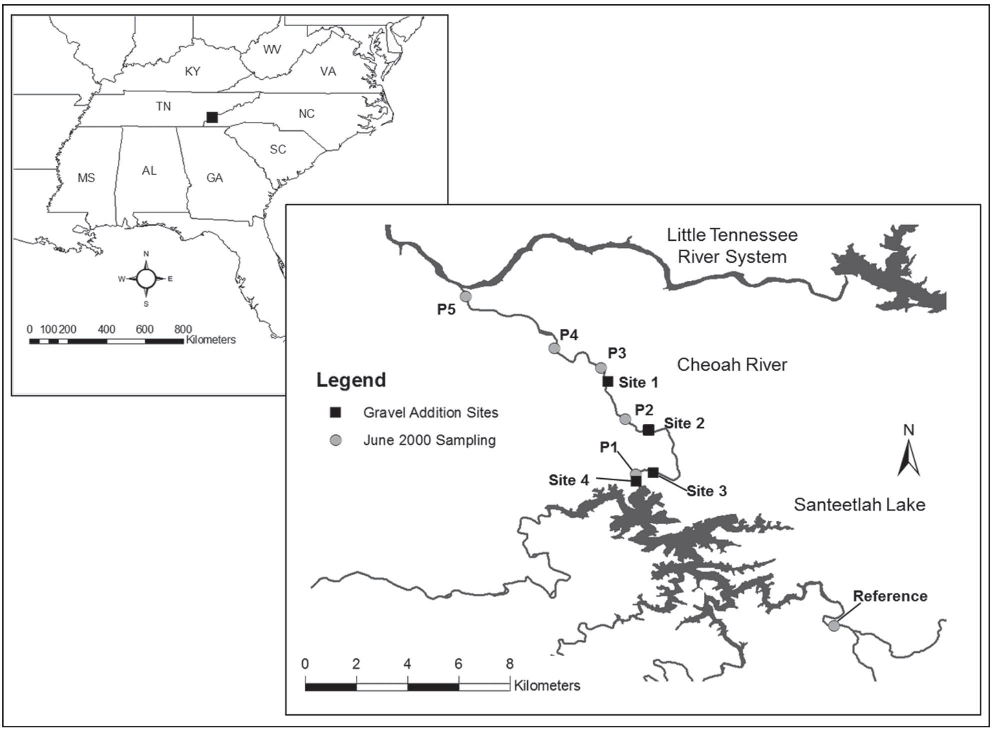

Figure 1. Map of gravel addition sites (sites 1–4) and sites sampled by Pennington and Associates (Reference and P1-P5) in June 2000 in Cheoah River. Because gravel transport was high and created poor treatment effects at sites 1 and 2, macroinvertebrate responses were only assessed at sites 3 and 4.

was limited to leakage from the dam (<0.002 $m^3 s^{-1}$), inputs from tributaries, and occasional large pulses (>24 $m^3 s^{-1}$) from the reservoir. The altered hydrology and sediment supply led to degraded habitat for many aquatic biota, including the federally threatened *Spiraea virginiana* Britton (Virginia Spiraea) and the federally endangered *Alasmidonta raveneliana* Lea (Appalachian Elktoe Mussel) (USFWS 1994). In March of 2005, the FERC issued the dam's new 40-year license, which required seasonally variable base flows between 1.13 $m^3 s^{-1}$ and 2.83 $m^3 s^{-1}$ and periodic high flow events (28.3 $m^3 s^{-1}$) (FERC 2005). The license also required that the lower river reaches be supplemented with at least 76.5 m^3 of gravel on a bi-annual basis.

During 21–23 February 2008, washed gravel was mined from drained floodplains of the Alabama River near Montgomery, AL, transported by dump trucks, and dumped down the stream bank into the Cheoah River channel at four sites, two of which were near the dam (Fig. 1). Sites with steep embankments were chosen to promote gravel migration into the channel. The rapid substrate entrainment at sites 1 and 2 (further downstream), however, led to sparse coverage of gravels on the stream bed (McManamay et al. 2010). Thus, we only evaluate the effects of gravel addition on macroinvertebrates at sites closest to the dam (sites 3 and 4). In addition, benthic surveys by Pennington and Associates (2001) showed that there were fewer macroinvertebrate families near sites 3 and 4 than sites than further below the dam (Fig. 1; Supplementary Appendix 1, available online at http://www.eaglehill.us/SENAonline/suppl-files/s12-3-1138-McManamay-s1, and, for BioOne subscribers, at http://dx.doi.org/10.1656/S1138.s1). Hence, we presumed that these sites would display the most noticeable biological effects of restoration. Site 4, located 0.25 km downstream of the dam, consisted of a 34-m-wide riffle/run habitat with moderate stream gradient (0.58%). Site 3, located 0.75 km downstream from site 4, consisted of a 22-m-wide slow glide with lower gradient (0.35%). Approximately 19 m^3 (40 tons) of gravel (particle size-range = 7.5–15 mm) were dumped down the bank at both sites.

Following gravel addition at each site, high-magnitude flows deposited newly added gravels halfway into the channel over the existing coarse streambed, and within our study's time frame, eventually 60 m downstream at both sites. Because gravel particles differed in coloration from existing native substrates, we were able to visually assess the spatial extent of the new gravel layer (McManamay et al. 2010). We classified areas of the streambed overlain with newly added gravels as "enhanced" and areas of coarse substrates not overlain with newly added gravels as "unenhanced". As more gravel migrated downstream from the pile following large flow events, enhanced areas increased in size.

Site physical characteristics

Streamflow was recorded daily during the entire study as discharge from the dam. Average daily spill records were provided upon request by Alcoa Power Generating, Inc. To capture differences in ambient conditions, we measured water depth and mean water column velocity at 0.6 X depth using a Marsh-McBirney model no. 2000 flow-meter and measuring rod across 10 locations at each site during baseflow conditions following gravel addition in June 2008. We established six transects perpendicular to the stream channel at 10 m intervals from the location of the gravel pile downstream. We conducted pebble counts by measuring the intermediate axes of 50 randomly selected particles along each transect before and after gravel addition (January 2008 and June 2008, respectively). We took 20 measurements of added gravel depths at equally spaced intervals along transects starting in April 2008 and periodically every season after for a year (i.e., June, November, and January 2009). Added-gravel depth was measured by forcing a metal measuring rod into the gravel substrates until the rod contacted the coarse and impenetrable pre-existing stream bottom. We used a modified Terhune Mark VI groundwater standpipe and volumetric pump to measure streambed permeability, which represents the volume of water pumped through streambed pores over time (McBain and Trush 2000). Streambed permeability was measured once during June 2008 by driving a standpipe into the substrate to a depth of 15 cm at 10 locations within enhanced and unenhanced areas at each site (locations were selected where gravels were sufficiently deep to attain a permeability reading). A depth of 15 cm is the standard shallow depth for inter-gravel measurements (Merz and Setka 2004, Sarriquet et al. 2007). At each location, we recorded the average value of three readings taken for a duration of 20 seconds each. Measurements of pumped volume per time were also taken for above streambed conditions (i.e., not inter-gravel) at every fifth location to determine if our intergravel readings were accurate or if pump battery power was low. Streambed permeability (cm hr^{-1}) was calculated from inflow measurements (ml s^{-1}) and corrected for temperature (viscosity differences) using calibration curves from McBain and Trush (2000).

Macroinvertebrate response

Because we knew the location of gravel additions and the projected path of enhancement, we were able to collect macroinvertebrate and substrate samples in both treatment areas of the streambed before and after gravel addition. At each gravel-addition site, five macroinvertebrate samples were collected within the enhanced areas, and five more within the unenhanced areas one month before gravel enhancement (January 2008) and periodically every season after gravel enhancement for a year (i.e., April, June, November 2008, and January 2009). Macroinvertebrate sampling was intended to capture the range of microhabitat complexity (e.g., various gravel depths and substrate size ranges). Macroinvertebrate samples were collected by placing a 0.25-m^2-quadrat along one of five fixed transects and disturbing the sediment to a depth of 15 cm (if possible, given the armored stream bottom, e.g., underlying bedrock) upstream of a 500-µm mesh square kicknet for 30 seconds. Samples were placed in sealed plastic bags with 95% ethyl alcohol. Macroinvertebrates were identified to the family level using a dissecting microscope, and each organism was assigned to a functional feeding group according to the criteria of Merritt and Cummins (1996)—collector-filterer, collector-gatherer, predator, scraper, shredder, and piercer herbivore.

Substrate microhabitat

We also measured the intermediate axis of eight random particles within each 0.25-m^2-quadrat. We calculated the median particle size (D_{50}), as well as the substrate heterogeneity index, which is the number of various substrate size classes represented in the eight substrate measurements for each 0.25-m^2-quadrat. The substrate size classes represented sand (> 2mm), small/medium gravel (2–16 mm), large gravel (16–64 mm), small cobble (64–128 mm), large cobble (128–256 mm), small boulder (256–512 mm), large boulder (512–4096 mm), and bedrock. The substrate heterogeneity index range was 1–8.

Statistical analysis

We used Kruskal-Wallis ranked sum tests to compare particle sizes from pebble counts conducted pre- and post-gravel addition, average streambed permeability in enhanced and unenhanced areas, and substrate microhabitat variables in enhanced and unenhanced areas at both sites. We tested for the effect of gravel enhancement on overall density (indviduals m^{-2}), Shannon's diversity (H), evenness (J), family-level richness, and the density of individuals within various functional feeding groups across time using repeated-measures MANOVA in JMP (SAS Institute, Cary, NC). We also tested for the effect of gravel enhancement on the density of the 10 most dominant taxa over time. We nested gravel enhancement within site (site[gravel enh.]) while also testing for the effects of gravel enhancement separately. Macroinvertebrate responses at different time periods are used as multiple variables in our analyses. Thus, repeated measures MANOVA takes into account the effect of time as correlations among all responses and the interaction of time with other effects (Zar 1999). In addition, MANOVA is robust with respect to outliers and does not assume sphericity or equal variances at every time period (Zar 1999). We evaluated the effects of time and all interaction effects with time. We focused primarily on the statistical results of time interaction effects to determine if gravel addition had genuine effects on the macroinvertebrate community or if the effects were an artifact of pre-existing sampling locations. We hypothesized that the ecological responses might change over time. We also used linear contrasts to compare responses within enhanced gravels at each time period to the pre-restoration time period (i.e., January 2008). Because of non-normality, the count data were transformed using sqrt(x+3/8) equation (Kihlberg et al. 1972, Zar 1999), whereas all other variables were log(x + 1)-transformed before statistical analysis (Zar 1999).

We used Spearman's rank correlations to evaluate relationships between density, H, J, and family-level richness, and D_{50} and substrate heterogeneity index in order to assess the influence of substrate microhabitat and pre-existing conditions on the effectiveness of habitat restoration. We evaluated two different datasets: one dataset consisted of only the unenhanced samples, which represented the pre-existing condition of the stream bed, and the other dataset contained all data, which represented the additional influence of enhanced conditions.

We used non-multi-dimensional-scaling (NMDS) to assess the effect of gravel enhancement on macroinvertebrate community composition. We used Bray-Curtis dissimilarity of relative family densities (i.e., proportions) to ordinate our samples. The values were arcsin-square-root-transformed before ordination. The NMDS provides a visual representation of the dissimilarity in community composition of samples from enhanced and unenhanced samples with respect to different sites and different time periods. We used the metaMDS function (vegan package) in the R programming environment to ordinate samples using 100 different initial configurations and 200 maximum iterations (Oksanen et al. 2012). Although the metaMDS function provides a best solution (number of dimensions), we repeated the function for different numbers of dimensions and visually evaluated the scree plot of stress values compared to dimensions to ensure that our final solution was robust. As a secondary measure, we also compared biplots of dissimilarity versus ordination distance to determine strength (variation explained) of different solutions with varying dimensions using linear regression. To interpret ordination axes, we assessed relationships between relative family densities and NMDS axes using Spearman's rank correlations.

Results

Site physical characteristics

Following additions, gravel migrated 56 m downstream and as much as 15 m from the bank into the channel at site 3. Gravel migrated 73 m downstream at site 4 and up to 13 m into the stream channel. Stream velocity at site 3 averaged 0.047 m s^{-1} (SE = 0.012), whereas water depth averaged 0.53 m (SE = 0.032). The average stream velocity at site 4 was higher than that of site 3 and averaged 0.42 m s^{-1} (SE = 0.070), whereas average water depth was similar at the two sites (average = 0.63 m, SE = 0.013). The average gravel depths within each time period varied very little and ranged from 6.30 to 8.74 cm (SE = 1.32) at site 3, and 5.62 to 8.68 cm (SE = 1.57) at site 4. The maximum gravel depths at both sites occurred during November and peaked at 28.8 cm at site 3 and 40.0 cm at site 4.

Extreme high-flow events occurred during February–March 2008 (>130 m^3 s^{-1}) and on 7 January 2009 (232 m^3 s^{-1}), which coincided with the largest changes in gravel depths. Smaller-magnitude high-flow pulses (≈30 m^3 s^{-1}) occurred in late March through early May 2008 and led to smaller shifts in gravel depths. Little change in gravel depth occurred during the summer and late fall and corresponded with low streamflows.

The particle size distributions were significantly smaller after gravel addition at site 3 (X^2=14.67, df =1, $P = 0.001$), but were not significantly different at site 4 (X^2 = 1.530, df = 1, $P = 0.216$). The average streambed permeability in enhanced gravels at site 3 was significantly higher (168.8 cm hr^{-1}, SE = 13.99) than in the unenhanced gravel reaches (115.9 cm hr^{-1}, SE = 12.88) (X^2 = 7.823, df = 1, $P = 0.0052$). The average streambed permeability in enhanced gravels at site 4 was also significantly higher (182.4 cm hr^{-1}, SE = 3.037) than in the unenhanced gravels (88.07 cm hr^{-1}, SE = 12.17) (X^2 = 21.80, df = 1, $P < 0.0001$).

Substrate microhabitat

In contrast to pre- and post-enhancement particle size distributions, the median particle sizes within enhanced areas were significantly smaller than unenhanced areas at both site 3 and site 4 ($X^2 = 181.5$, df = 1, $P < 0.0001$; $X^2 = 19.78$, df = 1, $P < 0.0001$, respectively). However, the effect of gravel enhancement on substrate microhabitat size at site 3 was greater than at site 4 (Fig.2).

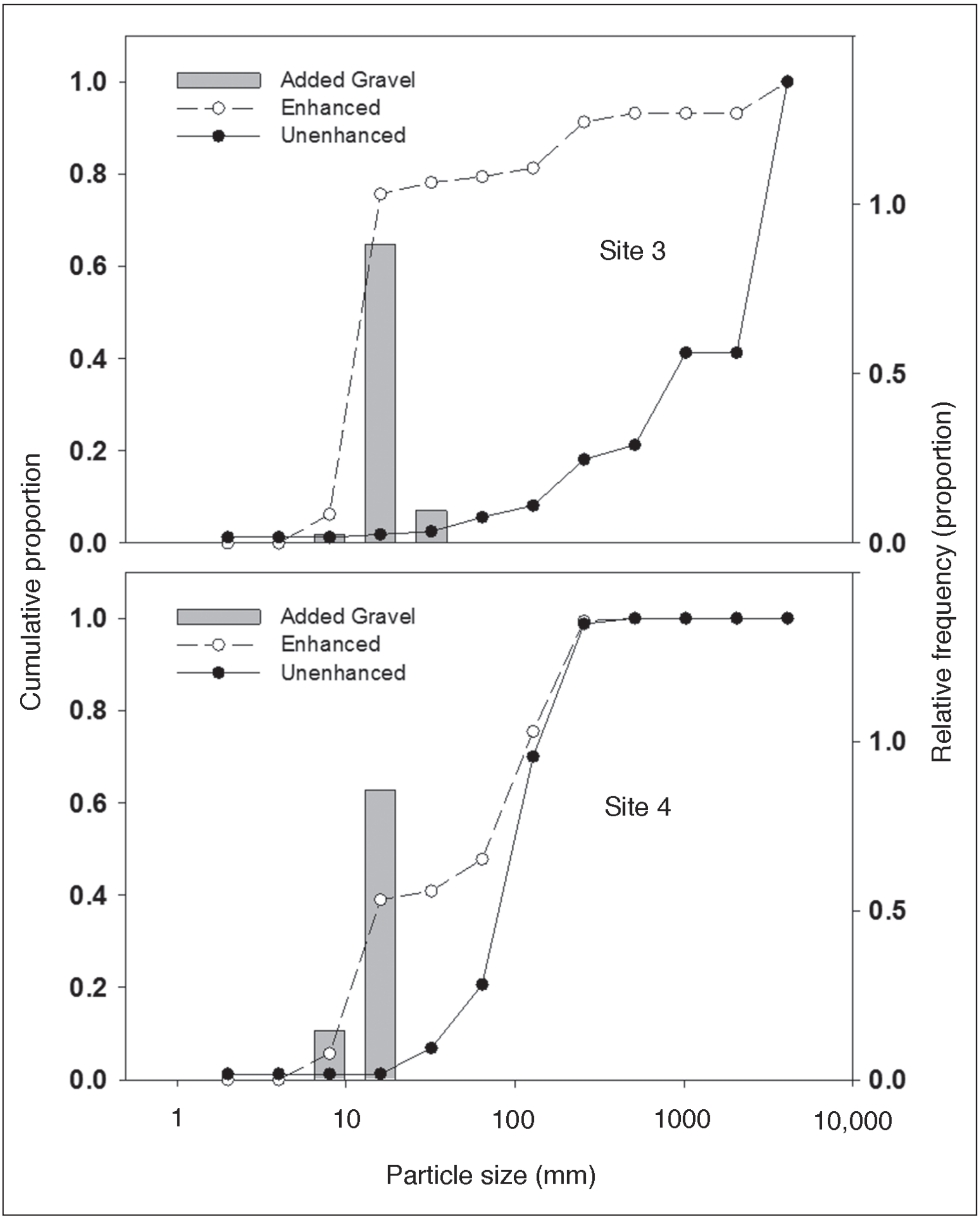

Figure 2. Particle size distributions for pebble counts within enhanced and unenhanced microhabitats (left axis) and the relative frequency of augmented gravel sizes (right axis) at study sites.

Substrate heterogeneity was not significantly different between treatments at site 3 ($X^2 = 2.763$, df = 1, $P = 0.097$) but was significantly higher in enhanced areas at site 4 ($X^2 = 14.26$, df = 1, $P = 0.0002$).

Macroinvertebrate responses and relationships with substrate

A total of 41 families of macroinvertebrates were collected from our sites during the study (Supplementary Appendix 1). In general, the responses by the macroinvertebrate community were not consistent during the study. Family richness, H, and J were higher in enhanced gravels following gravel addition, except in January 2009 (family richness) and June (H and J) (Fig. 3, Table 1). In contrast, density (individuals m^{-2}) was only higher in enhanced gravels during June (Fig. 3). The effects of time interaction on overall density and J were significant. The most evident changes, however, occurred during June and January 2009 (Fig. 3). Family richness was significantly higher in enhanced gravels during April and June (Fig. 3). Time interaction effects of family richness, however, were not detected (Table 1). H was significantly higher in April and January 2009 (Fig. 3) and displayed significant time*site[gravel enh.] effects (Table 1). The densities for 8 of the 10 most abundant families were significantly affected by time interactions (Table 1,

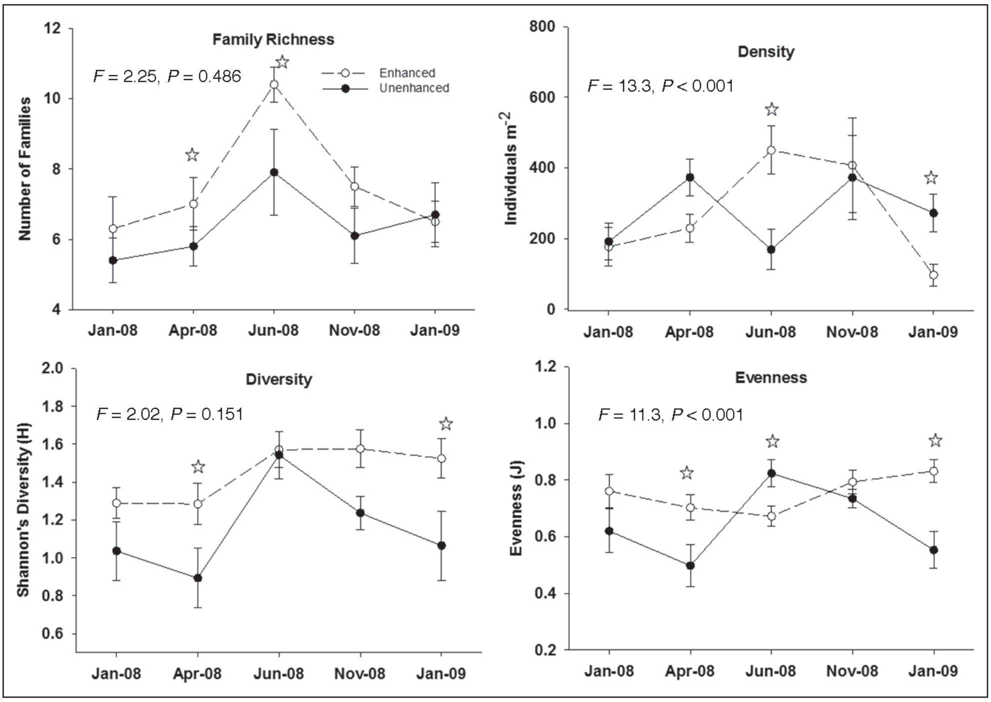

Figure 3. Mean family richness, density, diversity (H), and evenness (J) of macroinvertebrates within enhanced and unenhanced areas at both sites. Statistical results of time•gravel enhancement interactions from the repeated measures MANOVA models are presented. Each point represents the average among 10 samples within each treatment. Error bars indicate 1 SE. Star indicates statistical significance of enhancement at each time period from pre-enhancement conditions based on linear contrasts ($P < 0.05$).

Supplementary Appendix 1). Members of Coenagrionidae, Heptageniidae, Physidae, Planorbidae, and Sphaeridae had significantly higher densities in enhanced gravels during June. Members of Chironomidae, Simuliidae, and Hydropsychidae had lower densities in enhanced gravels and showed variable seasonal trends (Supplementary Appendix 1).

Among functional feeding groups, collector-filterer, collector-gatherer, and predator densities were significantly affected by time interactions (Table 1) and had lower or similar densities in enhanced areas than in unenhanced areas. The exception was in June when collector-filterer, collector-gatherer, and predator densities were much higher in the enhanced areas than in the unenhanced areas (Fig. 4). The density of scrapers, although not significantly affected by time interactions, also peaked in June, with slightly higher densities in the enhanced areas. Site location had significant effects on all functional feeding groups, except for shredders and piercer-herbivores, and most likely influenced the response to gravel addition (Table 1). For example, the densities of collector-filterers were

Table 1. Statistical results for repeated measures analysis of variance for 20 models including: composite macroinvertebrate community responses, the density of 10 dominant families, and the density of 6 functional feeding groups. Values represent *F*-statistics. Site[Gravel Enh.] indicates gravel enhancement treatment is nested within site. • = an interaction.

	Between subjects			Within subjects			
	All between model	Site [Gravel Enh.]	Gravel Enh.	All within^{A} model	Time	Time• Site[Gravel Enh.]^{A}	Time • Gravel Enh.
df	3	2	2	12	4	8	4
Density	3.94*	5.87*	0.09	4.01***	1.6	5.07**	13.3***
Family richness	10.3***	12.4**	6.06*	1.83	1.86	2.14	2.25
Shannon's diversity (H)	22.6***	21.0***	25.7***	2.79*	5.25*	4.79**	2.02
Evenness (J)	4.63*	2.26	9.37*	3.60**	6.58**	6.34***	11.3***
Chironomidae	4.30*	0.68	11.5**	1.54	44.1***	0.74	5.76*
Coenagrionidae	11.0***	6.55*	19.9***	2.17*	22.0***	2.01	3.11*
Heptageniidae	31.6***	42.5***	9.80*	1.6	5.76*	2.34*	0.91
Hydropsychidae	17.9***	26.9***	0.04	1.09	7.72**	0.61	2.17
Philopotamidae	11.4***	17.0***	0.28	1.94	45.6***	3.12*	0.68
Physidae	7.41**	4.00*	14.2**	2.25*	42.5***	1.57	10.4***
Planorbidae	31.9***	29.5***	36.6***	1.62	17.6***	2.51*	8.67**
Polycentropodidae	4.59*	6.25*	1.27	0.87	1	1.23	0.15
Sphaeriidae	14.7***	12.4**	19.5***	1.6	18.3***	1.86	5.45*
Simuliidae	41.5***	59.6***	4.94*	3.46**	42.4***	4.48**	3.1
Collector-filterers	17.2***	25.8***	0.03	1.93	7.98**	2.37*	1.54
Collector-gatherers	5.41*	7.20*	1.81	2.45*	25.3***	3.18*	27.9***
Piercer-herbivores	3.19	0.61	0.5	2.74*	24.5***	0.3	1.76
Predators	10.6***	9.90**	12.0**	3.36**	31.4***	3.35*	3.57*
Scrapers	56.0***	80.4***	7.13*	1.31	6.366**	2.03	0.19
Shredders	0.61	0.81	0.21	0.8	4.74*	0.31	1.9

^{A}*F*-statistic is approximated from Wilk's lamba values; *, **, and *** = significance at alpha = 0.05, 0.005, and 0.0005 levels, respectively.

higher at site 4, whereas collector-gatherer densities were higher at site 3 (data not shown). In addition, predator densities became higher in the unenhanced areas at site 4 in November 2008 and January 2009, but this was not observed at site 3. Although insignificant, shredders became absent or rare in samples from enhanced gravels, but were present in the unenhanced areas (Fig. 4). Piercer-herbivores became rare by November and were absent by January 2009 in both the enhanced and unenhanced areas (Fig. 4).

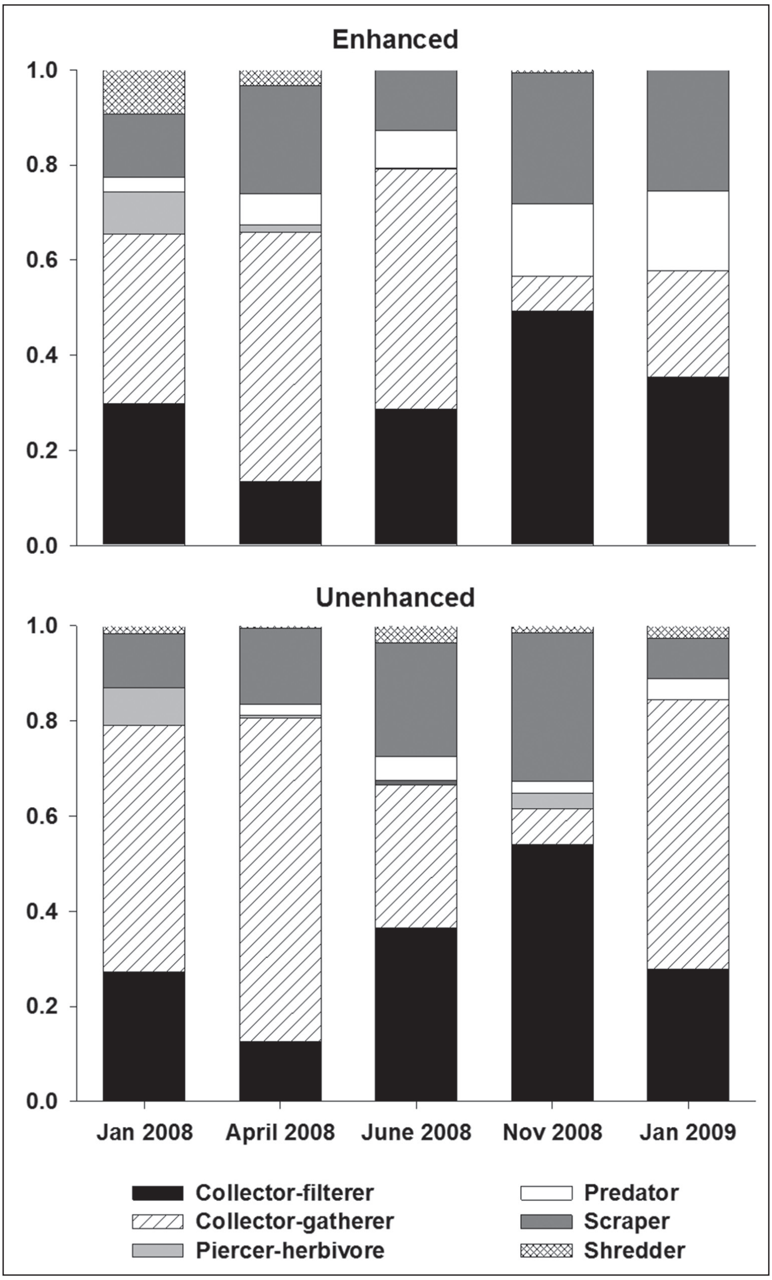

Figure 4. Stacked-bar charts of functional feeding group composition (proportions) in enhanced and unenhanced areas across both sites during each sampling period.

When considering unenhanced and enhanced data together, family richness, H, and J were significantly negatively correlated with D_{50}, whereas family richness and H were significantly positively correlated with substrate heterogeneity (Table 2). We observed similar correlations when considering only the unenhanced data (Table 2). Family richness and H displayed significant negative relationships with D_{50}, whereas both variables showed significant positive correlations with substrate heterogeneity (Table 2).

The NMDS ordination showed that the best statistical solution was reached at three dimensions with a stress of 0.1292. Biplots of dissimilarity versus ordination distance had r^2 values of 0.84 for two dimensions, 0.9 for three dimensions, and 0.93 for four dimensions, which suggested that adding more than three dimensions did not explain substantially more information. We plotted only the first two NMDS axes for visual representation. Macroinvertebrate communities were similar across sites and showed little divergence related to gravel addition, except for the June and November samples at site 3, and the June sample at site 4 (Fig. 5). Chironomids, on average, composed 29.1% of the relative density (RD) in samples and displayed a significant negative correlation with NMDS 1 (Fig. 5). On average, hydropsychids and heptageniids composed 13.9 and 15.8% of the RD, respectively, and both displayed significant negative correlations with NMDS 2 (rho = -0.77, -0.62, respectively, $P < 0.0001$; Fig. 5). Coenagrionids. planorbids, and sphaerids (RD = 3.9, 1.6, 2.9%) displayed positive correlations with NMDS 1 (rho = 0.59, 0.53, 0.52, $P<0.0001$). Philopotamids and physids (RD = 6.3, 6.1%) displayed negative and positive correlations, respectively, with NDMS 2 (rho = -0.55, 0.62, $P < 0.0001$).

Discussion

Following gravel addition, only two of the four sites displayed sufficient physical treatment effects to warrant further investigation to assess macroinvertebrate responses. At these two sites, our results suggested that the macroinvertebrate responses to gravel addition were not consistent or sustained, at least not within the temporal extent of our study. Within two months following the initial gravel addition at both sites, gravel migrated rapidly into the channel,

Table 2. Spearman's rank correlation matrix for macroinvertebrate composite response variables versus substrate microhabitat variables. Values represent Spearman's rho. *, **, and *** indicate significance at alpha = 0.05, 0.005, and 0.005 levels, respectively.

Substrate microhabitat	*n*	Family richness	Density	H	J
Unenhanced and enhanced	100				
D50		-0.40***	-0.07	-0.44***	-0.22*
Substrate heterogeneity		0.23*	0.04	0.32**	0.17
Unenhanced only	60				
D50		-0.43**	-0.18	-0.43**	-0.14
Substrate heterogeneity		0.42**	0.14	0.47***	0.18

leaving on average a 6 cm layer of homogenous, 7.5- to 15-mm-diameter sediments over approximately half the channel. We found that gravel addition caused shifts in the particle size within the enhanced areas, and increased the permeability of the streambed. Similar to other studies, we found that macroinvertebrates quickly colonized the new substrates following the initial habitat modification (Brooks and Boulton 1991, Merz and Chan 2005).

Despite changes in streambed conditions, the macroinvertebrate responses were taxon-specific, depending on site-specific conditions and upon season. We observed some significant patterns in a few macroinvertebrate families. Most responses, however, were season-specific. For example, shifts in community composition were different between sites 3 and 4, with the most evident changes occurring in June and November. Specifically, chironomids seemed to be negatively associated with gravel enhancement at site 3. In contrast, coenagrionids, physids, planorbids, and sphaerids displayed increases in enhanced gravels with peaks occurring in June and November.

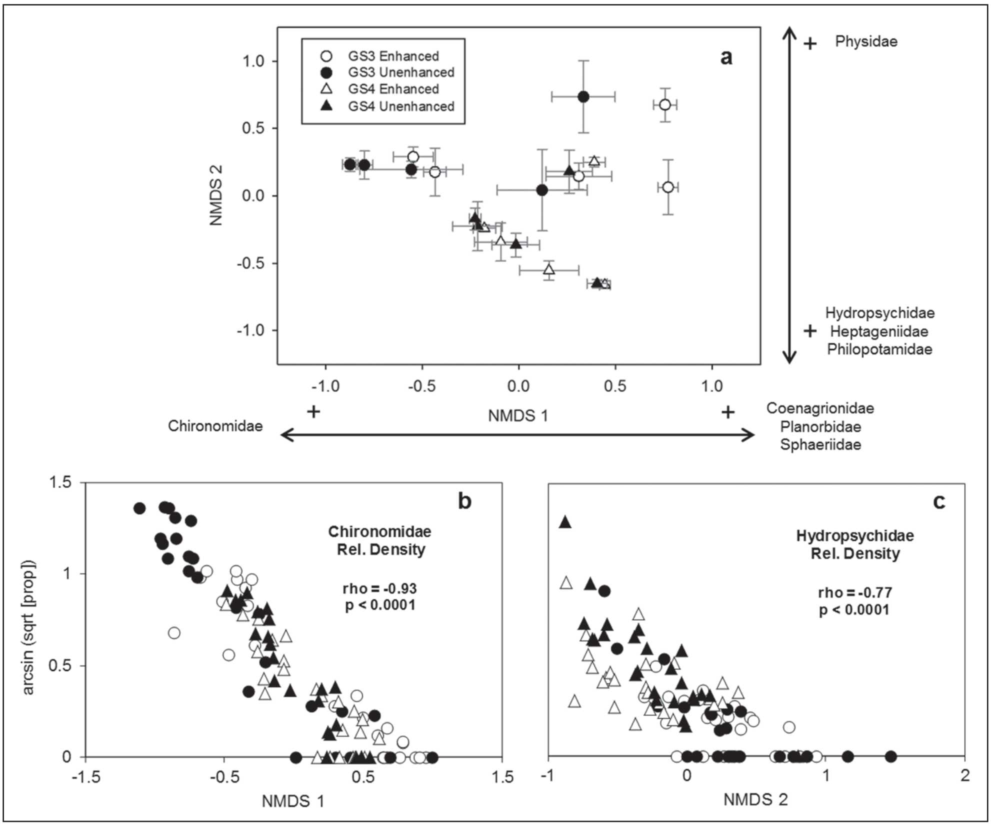

Figure 5. (a) Non-metric multi-dimensional scaling (NMDS) scores for all samples according to site and treatment (enhanced versus unenhanced). Points represent the mean score for each time period and error bars indicate 1 SE. Arrows indicate direction of increasing relative densities of families that explained the most variation in NMDS axes 1 and 2. Examples of biplots and Spearman correlation rho values between (b) chironomid relative density and NMDS 1 and (c) hydropsychid relative density and NMDS 2.

Shifts in the community structure suggested possible changes in food availability and habitat preference for some functional feeding groups. Peaks in collector-gatherers, predominately physid and planorbid snails, may have corresponded to higher food availability in enhanced gravels (Hill et al. 1995, 2001). For example, during June at site 3 we observed a mixture of algal and fine organic matter along with macrophytic vegetation on the enhanced gravel surface. Increases in particulates may also explain why there were peaks in the abundance of sphaerid clams. Similarly, Merz and Chan (2005) found an increase in collectors in newly augmented gravels, which suggests that there was an increase in either habitat or food. Although we found an increase in collectors, shredders decreased in abundance.

Interestingly, Merz and Chan (2005) found that predators were less abundant in augmented gravels compared to reference sites. However, we observed higher densities of predators such as coenagrionids in enhanced gravels during June. Coenagrionids, which are commonly associated with aquatic vegetation (Merrit and Cummins 1996), may have been influenced by the increase in aquatic macrophyte coverage, primarily *Cabomba caroliniana* Gray (Carolina Fanwort), at site 3; at site 4, which also had a peak in coenagrionid density, faster water velocities were unsuitable for *Cabomba*, which was absent. Thus, a plausible explanation is that peaks in predator densities may have resulted from increases in cover or increases in prey availability in enhanced gravels.

Comparisons with other studies

The biologic effectiveness of restoring habitat heterogeneity has recently received considerable attention, yet habitat restoration trials have had mixed results (Lepori et al. 2005a, Merz and Chan 2005, Miller et al. 2010, Muotka and Laasonen 2002, Muotka et al. 2002, Sarriquet et al. 2007). Increasing habitat heterogeneity has been shown to enhance ecosystem processes such as organic matter retention (Lepori et al. 2005b, Muotka and Laasonen 2002). However, the linkages between restored processes and functional responses are poorly understood. Miller et al. (2010) completed a meta-analysis of published articles assessing macroinvertebrate responses to in-stream habitat restoration and found that large woody debris additions and boulder additions significantly increased macroinvertebrate richness from unrestored conditions. Only one of the 24 studies in Miller et al.'s (2010) analysis specifically assessed the effects of gravel additions, wherea 10 studies evaluated effects of large-structural additions (i.e., boulder placement) or riffle construction. We found only three peer-reviewed articles and one government report documenting macroinvertebrate responses to gravel addition (Table 3). Thus, there is a paucity of information in the published literature to inform future restoration efforts using gravel addition. Three studies concluded that species richness was either not influenced or decreased following gravel addition (Merz and Chan 2005, Sarriquet et al. 2007, Watry and Merz 2009), whereas only one study reported increases (Albertson et al. 2010) (Table 3). We found

Table 3. Site summary information, restoration application, and biotic responses from the current study and four other studies assessing the effects of gravel addition on macroinvertebrates. The total amount of added refers to the cumulative volume of gravel augmented to all reaches. Notes/response follow the summary info for each study.

Reference	Location	Drainage area (km^2)	Cause of degradation	Total amount added (m^3)	Gravel depth (cm)	Size (mm)	No. of reaches	Sample period (months)
This study	Cheoah River, NC	550	Dam regulation	38	6	7.5–15	2	12
Density and richness responses were not sustained. Responses were specific to site conditions and substrate microhabitat. Shifts in taxonomic composition. Gravel mobility an issue.								
Merz and Chan (2005)	Mokelumne River, CA	1624	Dam Regulation	380–1200	40	25–150	7	6
Density significantly higher but richness lower in augmented gravels. Shifts in taxonomic composition.								
Watry and Merz (2009)	American River, CA	4921	Dam regulation	3593	-	8–89	1	12
Density higher but richness lower in enhanced gravels. Shifts in taxonomic composition. Gravel mobility was high and possibly an issue.								
Albertson et al. (2010)	Merced River, CA	2748	Dam regulation	1.0E6	-	53	4	14
Density lower but richness higher in enhanced gravels. Shifts in taxonomic composition. Gravels that were mobile led to lower density and richness and may have influenced taxonomic composition.								
Sarriquet et al. (2007)	Tamoute River (France)	1.3	Agriculture	-	15	15–30	1	29
No changes in density or richness. Shifts in taxonomic composition.								

one peer-reviewed paper reporting increases in macroinvertebrate richness in response to experimental manipulations of substrate size and heterogeneity (Brooks et al. 2002). In contrast to species richness, three of the four studies showed increases in macroinvertebrate density following gravel addition, with Merz and Chan (2005) reporting dramatic increases. All gravel addition studies reported shifts in macroinvertebrate taxonomic composition.

Limits to restoration and implications for management

Increases in biotic diversity are rarely documented following habitat restoration treatments (Lepori et al. 2005a, Louhi et al. 2011, Merz and Chan 2005, Muotka and Laasonen 2002, Sarriquet et al. 2007). This lack of biological response may be a function of time needed for the immigration and colonization of new species from other areas (Miller and Hobbs 2007, Spanhoff and Arle 2007). Miller et al. (2010), for example, found that increases in macroinvertebrate richness to in-stream habitat restoration were more evident in samples taken after one year than in earlier post-treatment samples. Our results suggest that the temporal extent of our study and number of sites (i.e., sampling effort) were not responsible for the observed lack of macroinvertebrate responses to gravel addition. In contrast, our results suggest that site and microhabitat conditions, habitat stability, and the restoration application were more important in determining macroinvertebrate responses. For example, we found significant relationships between macroinvertebrate diversity (richness, H) and substrate variables (D_{50}, heterogeneity) when considering only the unenhanced locations (Table 2). This finding suggests at least two factors may be often overlooked in stream restoration studies: 1) substrate microhabitat may be as much or more important than overall site treatment effects, and, 2) relationships between macroinvertebrates and substrate microhabitat are most likely present before gravel addition. Thus, one limitation of restoration, albeit an obvious one, is that habitat restoration may be constrained by existing habitat-biotic relationships in the river system, such as organic inputs (Lepori et al. 2005b). If this is the case, then habitat enhancement may not increase biotic diversity unless it either dramatically influences the endpoints of the existing relationship or influences ecological processes via habitat manipulation (i.e., create new relationships). Brooks et al. (2002) argued that many restoration projects are conducted under the assumption that reach-scale manipulations focused to maximize physical habitat heterogeneity may not increase variability in local habitat parameters. Because macroinvertebrates may show substantial affiliation with local controls, i.e., microhabitat (Gurtz and Wallace 1984), the high degree of uncertainty in benthic macroinvertebrate responses to restoration may not be surprising. In addition, assessment of within-site responses may be more appropriate than assessments evaluating mean responses across multiple sites. Alternatively, studies can statistically account for these site-specific effects.

The effectiveness of restoration may also be largely dependent upon the degree of habitat improvement in substrate conditions. The fact that macroinvertebrate communities are structured by substrate size and heterogeneity is well documented (Beisel et al. 1998, Gurtz and Wallace 1984, Williams and Smith 1996). There were higher amounts of sand and cobble at site 4 before gravel addition, whereas site 3 was dominated by bedrock and boulders (>500 mm). In addition, higher water velocities at site 4 may have created more pre-restoration microhabitat complexity, leaving less room for enhancing habitat heterogeneity. Differences in enhanced and unenhanced substrate conditions at site 3 suggested a larger enhancement effect (Fig. 2), which may have led to more pronounced biotic responses. Three studies documented no change in benthic macroinvertebrate diversity following the addition of gravel over existing coarsened substratum (Merz and Chan 2005, Sarriquet et al. 2007, Watry and Merz 2009). However, Albertson et al. (2010) reported increases in macroinvertebrate richness in the Merced River, CA where the removal of 1.5 million tons of sediments was followed by replacement of new filtered substrates.

The disturbance regime of ecosystems also plays a key role in structuring macroinvertebrate communities (Brooks and Boulton 1991, Death and Winterbourn 1995, McCabe and Gotelli 2000). Following gravel augmentation, substrates may be highly unstable and prone to high-flow-mediated transport (McManamay et al. 2010, Watry and Merz 2009). Albertson et al. (2010) explicitly tested for gravel mobility effects on macroinvertebrates (induced via gravel augmentation) and found hydropsychid caddisfly abundance was lower in high gravel-mobility treatments. We found peaks in macroinvertebrate densities during the summer and fall, when gravel migration was low. Gravel instability may have influenced macroinvertebrates in two ways: 1) the consumers may have either become part of the bedload and were covered by new gravel sediments, or, 2) high flows flushed algal, particulate organic matter, and potential prey items from the gravel substrates, limiting food availability. The lower densities of sedentary collector-filterers, i.e., Hydropsychidae, Polycentropodidae, and Simuliidae, in enhanced gravels also suggest that these organisms avoid unstable gravel habitats.

We speculate that the lack of sustained macroinvertebrate responses at our sites was an artifact of the restoration design and substrate microhabitat. We say this for two reasons. First, the size range of augmented gravels was fairly homogenous and deficient of sand and fine gravel, thereby having minimal effects on habitat heterogeneity and creating highly mobile substrate conditions. Second, the small amount of added gravel (19 m^3 per site) did not result in an entire reach having multiple layers of heterogenous substrate. Rather, the enhanced areas encompassed only half of the stream and covered the existing armored stream bed with an average of 6 cm of gravel. Other studies report extensive volumes (380–1200 m^3 per site) of added gravels deposited in consistent layers (15–40 cm) over the streambed (Table 3). Habitat enhancement projects should be conducted as ecosystem experiments that will provide clear treatment effects, and advance the science of restoration (Palmer and Bernhardt 2006).

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