RESEARCH ARTICLE

Impacts of Channel Reconstruction on Invertebrate Assemblages in a Restored River

Lindsey K. Albertson,[1,2] Bradley J. Cardinale,[1] Steven C. Zeug,[1] Lee R. Harrison,[3] Hunter S. Lenihan,[3] and M. Aleksandra Wydzga[4]

Abstract

Ecosystem restoration often aims to recreate the physical habitat needed to support a particular life-stage of a focal species. For example, river channel reconstruction, a common restoration practice along the Pacific coast, is typically used to enhance spawning habitat for adult Chinook salmon, a species experiencing large population declines. These restoration efforts rarely consider, however, that altering spawning habitat could have indirect effects on other life-stages, such as juveniles, which might occur if, e.g. reconstruction alters the benthic food web. To determine how channel reconstruction impacts benthic macroinvertebrates, juvenile Chinook's primary prey, we conducted two studies at a restoration site in the Merced River, California. We asked (1) has gravel enhancement altered invertebrate assemblages in the restored reach compared with an unrestored reach? and, if so, (2) can shifts in the invertebrate community be explained by increased substrate mobility and by reduced heterogeneity that results from restoration? We show that invertebrate abundance and biomass were lower in the restored reach and that these changes were accompanied by a shift from dominance by filter-feeding caddisflies (*Hydropsyche*) in the unrestored reach to grazing mayflies (*Baetis*) in the restored reach. Using an in situ manipulation, we demonstrated that this trend was driven by increased substrate mobility that reduces the abundance of *Hydropsyche* and by decreased substrate heterogeneity that reduces the abundance of *Baetis*. Our studies suggest that geomorphic changes typical of reconstructed rivers can alter food webs in ways that may have important implications for supporting the focal species of restoration efforts.

Key words: disturbance, gravel augmentation, heterogeneity, macroinvertebrates, stream restoration.

Introduction

Ecological restoration has received increasing interest and funding over the past several decades, as degradation of natural systems by human activities has intensified. Most of these restoration efforts aim to recreate the physical and biological characteristics of degraded habitats so that historical populations can reestablish and become self-sustaining (Dobson et al. 1997; Vitousek et al. 1997). However, some recent critiques suggest that restoration efforts performed with this aim are often unsuccessful (Bernhardt et al. 2005; Palmer et al. 2005). In part, this is because restoration is conducted under the assumption that enhancing the structure of a habitat creates localized physical characteristics that are optimal for a target species (what has been called "the field of dreams" hypothesis [Palmer et al. 1997]). In addition, most restoration projects focus on creating physical habitat for just one life-stage of a focal species, a limitation that ignores the fact that countless organisms compose a system, and that even focal species may have various life-stages with different physical and biological requirements.

An example of restoration that focuses on one life-history stage stems from efforts to restore declining Chinook salmon (*Oncorhynchus tshawytscha*) populations in rivers along the west coast of the United States. Chinook salmon are an anadromous species that once supported a vibrant fishery with populations that ranged from southern California to Alaska. However, over the past several decades, populations of Chinook in California have dwindled (Yoshiyama et al. 2001), ultimately reaching record lows in 2007 and 2008 (PFMC 2008). There are a number of hypothesized causes of declining Chinook populations (Moyle 1994), and one that has received considerable attention is loss of spawning habitat in rivers due to altered flow regimes from damming and agricultural diversions. In an attempt to offset the loss of spawning habitat, considerable time and money have been spent on redesigning and enhancing channels to create river beds with rocks of the ideal size and shape to encourage adult spawning (Kondolf & Mathews 1993). Restoration projects generally restructure channels in ways that alter several key physical properties of

[1] Department of Ecology, Evolution & Marine Biology, University of California-Santa Barbara, Santa Barbara, CA 93106, U.S.A.
[2] Address correspondence to L. K. Albertson, email albertson@lifesci.ucsb.edu
[3] Bren School of Environmental Science and Management, University of California-Santa Barbara, Santa Barbara, CA 93106, U.S.A.
[4] Civil and Environmental Engineering, California Polytechnic State University, San Luis Obispo, CA 93401, U.S.A.

the river bed that are important for adult Chinook spawning, including homogenization of substrate by removing both fine particulates that might harm eggs and juveniles (Chapman 1988) and large boulders that hinder construction of redds. These restoration efforts additionally seek to enhance substrate sizes that exhibit natural mobility during bankfull floods so that gravel beds will remain suitable for salmon spawning over the long term (Trush et al. 2000).

What is rarely considered in restoration by channel reconstruction and gravel augmentation is how altering substrate mobility and heterogeneity might influence food web dynamics that indirectly affect other important life-stages of the focal species, such as juvenile fish. A long history of research in ecology has shown that the abundance, biomass, and diversity of species that support the base of a food web are strongly regulated by disturbance regimes (Sousa 1979; Resh et al. 1988; and others) and by habitat heterogeneity (Levin 1976; Pacala & Roughgarden 1982; and others). Disturbance is particularly important in streams and rivers that are subjected to large-scale flooding events that cause extensive loss of biota and resources (Fisher et al. 1982). Streams have served as an excellent system in which to explore the impact of disturbance on community-level patterns of diversity (Death & Winterbourn 1995) and species trait characteristics that influence, e.g. mechanisms of colonization (Mackay 1992) and use of physical habitat as refuge (Rempel et al. 1999; Matthaei et al. 2000). Habitat heterogeneity has also proven to be an important parameter determining community structure and diversity in streams (Vinson & Hawkins 1998; Beisel et al. 2000), and consideration of substrate composition and variation in streams has stimulated much interest in understanding how benthic organisms are distributed (Lamberti & Resh 1979; Richards et al. 1993) and respond to predation (Power 1992).

Here, we report the results of two studies designed to assess how changes in substrate mobility and heterogeneity in restored streams impact invertebrate assemblages that serve as the food-base for many native fish. Our studies were performed in a 2.7-km section of the Merced River in California's Central Valley that was recently reconstructed to enhance spawning habitat for populations of adult Chinook salmon. The questions that motivated our research were: (1) has channel reconstruction altered invertebrate assemblages in the restored reach of the Merced and, if so, (2) can shifts in the invertebrate community be explained by an increase in substrate mobility and/or a reduction in substrate heterogeneity in the restored reach? To address these questions, we monitored invertebrates in the restored reach of the Merced for more than a year and compared them with communities in a reach immediately upstream that was not altered by channel reconstruction. We then conducted an experiment in which we directly manipulated the mobility and heterogeneity of river bed substrates in situ to determine which, if either, of these two geomorphic factors could account for the shift in invertebrate assemblages in the restored reach. Collectively, our studies provide insight into how geomorphic variables affect the invertebrate portion of the food web, which may be an important factor to consider when restoring and managing river systems for the variety of life-history stages that influence the population sizes of focal species.

Methods

Study Site

Restoration of the Robinson reach (lat 37°29′N, long 120°28′W) occurred in 2001 as part of the Merced River Salmon Habitat Enhancement Project. During initial phases of restoration, approximately 1.5 million tons of sediment were removed from the river using heavy machinery and replaced with rocks that were sieved to create a gravel bed with median rock size of 53 mm in diameter. The stream channel and floodplain were regraded and resurfaced to produce a meandering, single-thread channel that contains alternating riffles and pools. Channel width (approximately 30 m), gradient, sinuosity, and bed texture were designed so that the river flow would generate bed-material transport to maintain riffles which are not clogged with fine sediment and which would be gradually reshaped into pointbars (CDWR 2005). We used a 1.3-km long upstream, unrestored reach (lat 37°29′N, long 120°28′W) that is immediately adjacent to the restored reach and experiences similar flow regimes as a reference with which to compare invertebrate communities in the restored reach. Although it would be ideal to have pre- and post-reconstruction data to conduct a before−after control-impact (BACI) analysis (Stewart-Oaten et al. 1986), funding and permitting constraints forced this project to start after the physical restoration was completed. Therefore, we used our next best alternative, a paired upstream reach that was physically and chemically similar in most respects, as a "reference" condition (see Table S1).

Pebble counts conducted in the unrestored and restored reaches have confirmed that channel reconstruction has indeed created substrate sizes that were slightly smaller (53 vs. 70 mm, D_{50}) and more homogeneous (0.00296 vs. 2.77, one standard error) in the restored reach versus the unrestored, reference reach (Fig. 1a). Harrison et al. (in revision) used these particle sizes in a spatially explicit flow model that was developed for, and validated at, this site. Based on the estimates of the Shields stress required to initiate particle movement, a greater fraction of bed materials in the reference reach was predicted to be mobile during high discharge events (Fig. 1b). Using these Shields values, we estimated the amount of time since restoration that the flow exceeds the discharge required to mobilize a certain fraction of substrates (Fig. 1c & 1d). At bankfull discharge (42.5 m³/s), which spans 9% of all days of record since channel reconstruction (Fig. 1d), Shields values indicated that 34% of bed materials in the restored reach were partially to fully mobile, compared to just 6.6% in the unrestored reach. At 75% of bankfull discharge (32.6 m³/s), which occurs on 11% of all days in the record, a minimum of 28% of the bed was partially mobile in the restored reach compared to 3.8% in the unrestored reach. At 15% of bankfull discharge (6.4 m³/s), which was exceeded on 71% of days since reconstruction, 5% of the bed was partially or fully mobile in the restored reach compared to near zero values
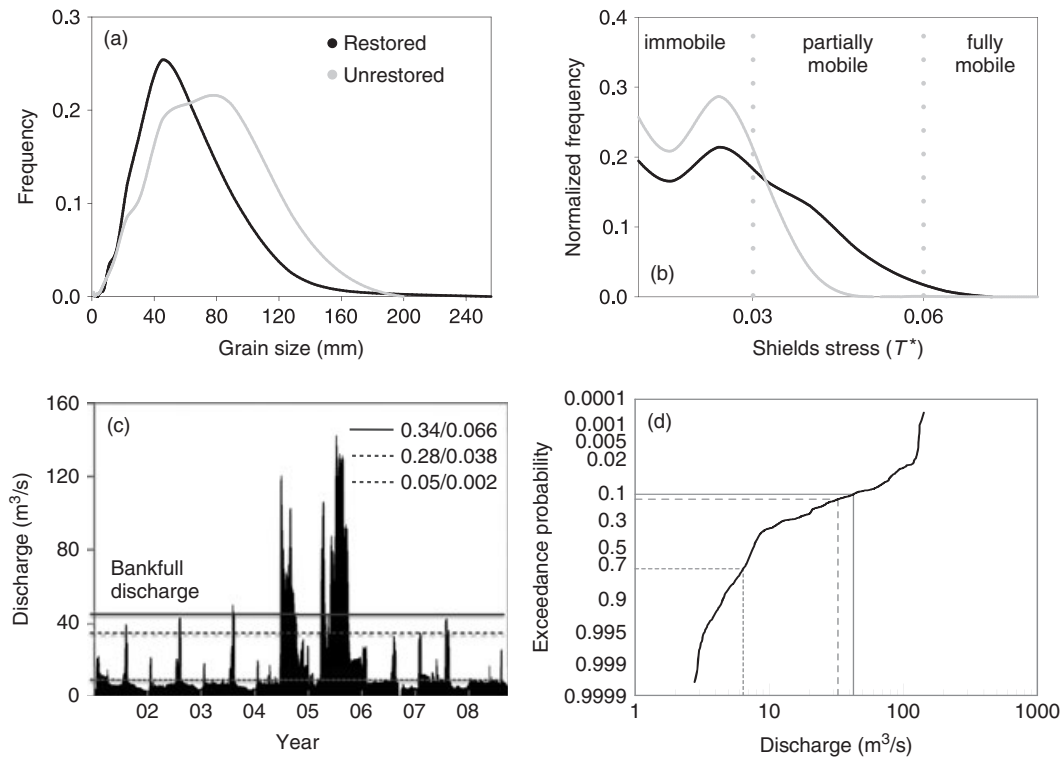
Figure 1. (a) Frequency distributions of grain sizes in the unrestored and restored reaches, determined by measuring the *b*-axis of a minimum of 100 particles in 24 and 17 counts in the unrestored and restored reaches, respectively. (b) Frequency distributions of bed mobility in the unrestored and restored reaches based on the estimates of Shields stress (τ *; Shields 1936) that were calculated from a two-dimensional flow model developed and calibrated at this study site by Harrison et al. Conventional bed mobility thresholds are shown at Shields values of 0–0.03 (immobile), 0.03–0.06 (partially mobile) and >0.06 (fully mobile) (Buffington & Montgomery 1997). (c) The mean daily flow discharge on the Merced River at the CADWR Snelling gage from 2001 to 2009 is shown to illustrate the frequency of bed mobilizing discharges. Horizontal lines correspond to bankfull flow (42.5 m^3/s, solid gray line), 75% of bankfull (32.6 m^3/s, long dashed gray line), and 15% of bankfull (6.4 m^3/s, short dashed gray line). Values at top right give the fraction of the bed that is mobile for the restored/unrestored reaches at the corresponding discharge, which ranges from 5 to 25× higher in the restored reach than the unrestored reach. (d) The streamflow duration curve indicates that bed mobilizing discharges of 42.5 (solid gray line), 32.6 (long dashed gray line), and 6.4 m^3/s (short dashed gray line) have been equaled or exceeded 9, 11, and 71% of the time in the post-restoration period. Thus, 5% of the bed is the restored reach that is at least partially mobile during 71% of all days and 28–34% of the bed is mobile during 9–11% of the time.

for the unrestored reach. Thus, the fraction of the bed that was mobile in the restored reach was 5–25 times higher than the reference reach depending on discharge. Furthermore, small fractions of the bed (5%) were mobilized almost weekly.

Monitoring

Macroinvertebrate assemblages were monitored approximately once per month from July 2007 until September 2008 in three riffles in the upstream, unrestored reference reach (hereafter called "unrestored") and in four riffles in the restored reach. Substrates in 1 m^2 patches of each riffle were sampled using a 500-μm mesh kicknet. Samples were preserved in 90% ethanol and processed by repeatedly counting invertebrates in X subsamples taken from our kicknet sample until a minimum of 100 individuals were enumerated and identified using Merritt and Cummins (1996). When 100 individuals were enumerated, the subsample was completed and the total abundance A_i of each species i per m^2 was calculated as $A_i \times X$. The bulk

weight of all individuals of each genus was then measured after being dried for 48 hours at 60°C to calculate biomass per square meter. We have previously found that this method is sufficient to ensure that we record even the rare invertebrate taxa.

We used mixed model repeated measures analysis of variances (ANOVAs) to compare the abundance, biomass, richness, and evenness of invertebrate assemblages between the two reaches using SAS, where reach was treated as a fixed effect and riffle location as a random effect. Because the amount of time between successive sampling dates varied, we used an autoregressive correlation structure (ARI) between dates that explicitly accounts for autocorrelation in the measurements among dates of differential spacing. In studies conducted in field settings, high variation between sampling replicates is often expected. Therefore, we decided to accept $p < 0.1$ as a significant effect. For the analyses, total abundance and biomass were natural log transformed to reduce heteroscedasticity.

We also compared community composition in the unrestored and restored reaches using distance-based non-metric multidimensional scaling (NMDS). We calculated distance matrices from relativized species densities using the Sørenson dissimilarity index (aka Bray–Curtis or Percent Dissimilarity, calculated as $1 - 2W/[A + B]$ where W is the sum of shared densities and A and B are the sums of densities in individual sample units (Sørensen 1948)). To test for significant differences in invertebrate community structure between reaches, we used the multi-response permutation procedure (MRPP) analysis in the software package PC-ORD (McCune & Mefford 2006).

Experiment

To determine whether increased substrate mobility and/or decreased substrate heterogeneity might explain shifts in invertebrate composition, we manipulated substrate mobility and heterogeneity in small patches in both the unrestored and restored reaches. The experiment was performed in both reaches to account for any differences in invertebrate assemblage composition that might exist a priori. Although we recognize that both the mean and variance of substrate sizes differed between the restored and unrestored reaches (as is evident in Fig. 1a), and that both the mean and variance of substrate sizes can have strong but differing impacts on invertebrates (Brooks et al. 2002), practical limits to the size of the experiment required that we focus only on substrate mobility and heterogeneity while holding the mean rock size constant.

Experimental units used in the study were 35 cm diameter $\times$ 8 cm high baskets made of 2.2 cm Vexar$^{\circledR}$ plastic mesh. The experiment was performed as a full 2×2 factorial having all combinations of substrate heterogeneity (homogeneous vs. heterogeneous) $\times$ substrate mobility (no mobility vs. mobility). Treatments of substrate heterogeneity were established by filling baskets with either substrates composed solely of the median rock size in the restored reach ($D_{50} = 53$ mm diameter) or a heterogeneous mixture of substrates diameter 22.6, 53, and 84 mm. The three size classes in the rock mixtures were chosen according to proportions found in the restored reach, which is roughly 43:7:1 (M. A. Wydzga, unpublished data). After filling the baskets with rocks, two baskets of each heterogeneity treatment were buried flush with the river substrate in each of five unrestored and five restored riffles (40 experimental units total). Experimental units were buried and left for invertebrates to colonize from 27 November 2007 through 12 January 2008, and then subjected to our second treatment of substrate mobility. One basket of each heterogeneity treatment at each riffle was randomly selected to be a treatment of "no mobility" and was left undisturbed. The second was assigned to a "mobility" treatment in which we simulated a bed-mobilizing flood by vigorously mixing and turning all rocks within the basket by hand. Substrate mobility simulations were conducted while snorkeling to ensure that no rocks that were manually agitated were lost from the basket. These events of substrate mobility occurred once on 12 January and once on 15 March 2008. The frequency and spacing of these events were constrained by two considerations. First, because it was not possible to continue the experiments through the spring flood, our experimental manipulations needed to be applied within the 4-month intervals between the fall (November) and spring (April) near-bankfull floods that typically occur in the Merced River. Second, we did not want to simulate the daily, or even weekly, disturbances that move 5% of the bed near base flow (Fig. 1c & 1d, short dashed line) as the lack of invertebrates in patches with such a frequent disturbance would likely prove biologically trivial. Therefore, we chose to mimic a disturbance that falls between these two extremes—one that was less frequent than the small rearrangements of bed materials that occur at 15% of bankfull flow (Fig. 1c & 1d, short dashed line) but which was more frequent than the large, relatively rare overbank flow events (Fig. 1c & 1d, solid line) that move over 30% of the bed and restructure channel morphology.

Invertebrates were sampled 4 weeks after the final disturbance on 12 April 2008 using a Hess sampler. The Hess sampler was designed to fit tightly around the diameter of the baskets so that only rocks within the baskets were sampled. Invertebrates in the baskets were dislodged by hand and subsequently caught in a 500-μm mesh collecting bucket attached to the Hess sampler frame. Kicknet samples were also taken on four sampling dates throughout the experiment in the same unrestored ($n = 3$) and restored ($n = 4$) riffles used in the monitoring study to establish background community composition in the two reaches. Invertebrate samples were processed as described previously.

We used general linear models to compare the total abundance, total biomass, species richness, and species evenness of invertebrate assemblages among treatment combinations using Systat11 for Windows. The full model included reach, heterogeneity treatment, disturbance treatment, and all higher order interaction terms. The most parsimonious model was selected by iteratively removing the least significant higher order interactions from the model. Abundance and biomass values were natural log transformed and proportion values were transformed by taking the arcsine of the square root to reduce heteroscedasticity.

We also performed multivariate analyses on community-level data from the manipulative experiment using distance matrices calculated from relativized species densities using the Sørenson dissimilarity index (as described previously). To test which taxa were driving trends in community structure in our experimental treatments, we used the indicator species analysis in the software package PC-ORD (Dufrene & Legendre 1997).

Results

Monitoring

Our year-long monitoring effort showed that invertebrate abundance was lower in the restored reach compared with the unrestored reach (Fig. 2a, $p = 0.08$). Average densities declined 19%, from $3,553 \pm 266$ individuals/m^2 (mean $\pm$ SE) to $2,874 \pm 222$, respectively. This decline was consistent
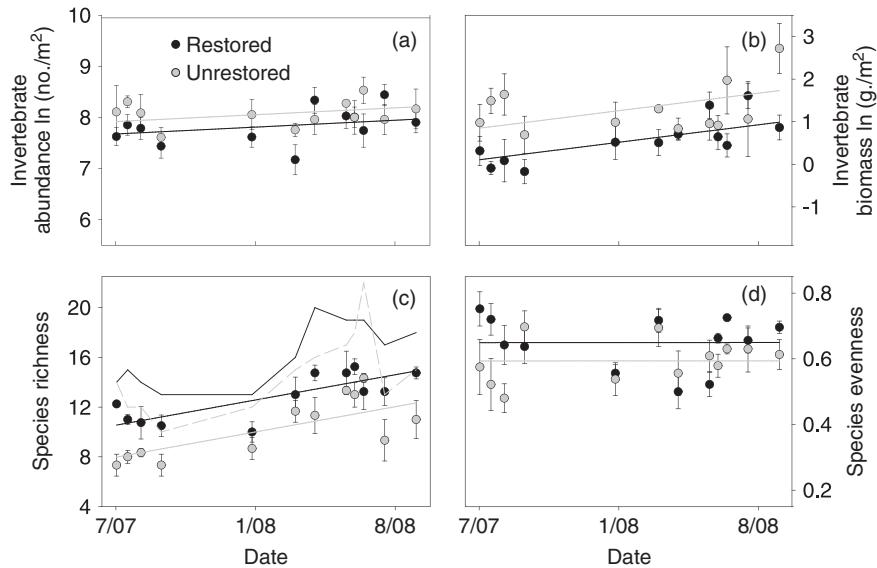
Figure 2. Community level patterns from invertebrate monitoring on 12 sampling dates from July 2007 to September 2008. Abundance (a, $p = 0.08$) and biomass (b, $p < 0.01$) are higher in the unrestored reach (gray dots and line), whereas species richness (c, $p < 0.01$) and evenness (d, $p = 0.03$) are higher in the restored reach (black dots and line). Values are mean ± 1 SE of $n = 3$ unrestored or $n = 4$ restored riffles on each date, and lines indicate the best-fit regressions. Black solid lines and gray dashed lines in panel (c) represent rarefied species richness in the restored and unrestored reaches, respectively. Table 1 shows the results from statistical analyses.

through time as indicated by the lack of any reach × date interaction. Biomass tended to increase over the duration of the study, but was also consistently lower in the restored reach (Table 1; Fig. 2b). This was represented by a decline ($p < 0.01$) from 6.1 ± 1.6 to 2.3 ± 0.3 g/m^2 in the unrestored and restored reaches, respectively. The two numerically dominant organisms at the study site were *Hydropsyche* and *Baetis*. *Hydropsyche* made up 37% of the assemblage in the unrestored reach and 17% of the assemblage in the restored reach, whereas *Baetis* made up 34% of the assemblage in the unrestored reach and 31% of the assemblage in the restored reach (Table 3). Other taxa present in the community at notable abundances were *Heptagenia*, *Chironomidae*, *Dugesia*, and *Tricorythodes* (Table 3).

In contrast to the observed declines in total abundance and biomass, species richness, and evenness (Fig. 2c & 2d) were higher in the restored reach compared with the unrestored reach (Table 1). Richness averaged 12.2 ± 0.4 in the restored reach and 10.1 ± 0.4 in the unrestored reach. Evenness averaged 0.661 ± 0.016 in the restored reach and 0.597 ± 0.017 in the unrestored reach. Because of the differences in total abundance between the two reaches, we used rarefaction to compare species richness for comparable levels of abundance (EcoSim7 Gotelli & Entsminger 2008). We found that, even after rarefying our samples, species richness was higher in the restored reach by approximately two species on all but one sampling date (Fig. 2c).

Ordination of community structure revealed distinct shifts in the composition of invertebrate assemblages between reaches and through time (Fig. 3a). The first two axes of the NMDS ordination explained 91% of the variation in the dataset.

Table 1. Results of statistical analyses showing differences in the abundance, biomass, and diversity of invertebrate assemblages among study reaches (unrestored vs. restored) over the sampling interval July 2007 to September 2008.

Dependent Variable	df	F	p
Total abundance (ln no./m^2)			
Reach	1,22	3.48	0.08
Date	1,29	2.6	0.1
Total biomass (ln g/m^2)			
Reach	1,22	14.89	<0.01
Date	1,29	10.97	<0.01
Species richness			
Reach	1,21	18.78	<0.01
Date	1,29	29.14	<0.01
Species evenness			
Reach	1,25	5.27	0.03
Date	1,32	<0.01	0.1

Results are from mixed model repeated measures ANOVAs where the most parsimonious model has been selected by removing higher order nonsignificant interactions.

The first axis primarily represented a seasonal shift in the grazing mayfly *Baetis* (Fig. 3c), which was nearly twice as abundant in winter ($1,359 \pm 181$ individuals/m^2) as in summer (909 ± 91 individuals/m^2). In contrast, the second axis of variation represented a significant difference ($p < 0.01$) in invertebrates between the unrestored and restored reaches. In particular, larval net-spinning caddisflies of the genus *Hydropsyche* were considerably less abundant in the restored reach ($F_{[1,15]} = 12.38$, $p < 0.01$), declining 63% from $1,304 \pm 1,080$ individuals/m^2 in the unrestored reach to 482 ± 103 individuals/m^2 in the restored reach (Fig. 3b).
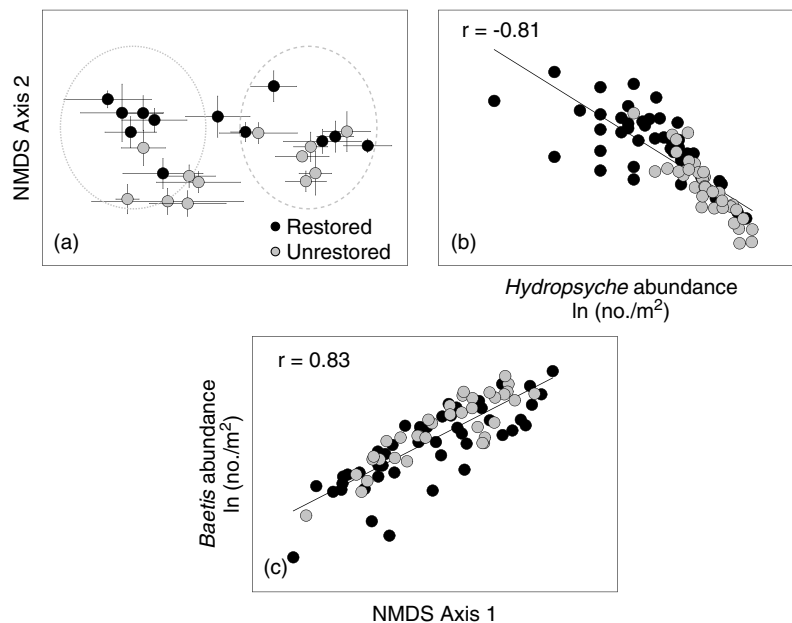
Figure 3. Results of multivariate community ordination from monitoring showing that invertebrate communities are significantly different between reaches (MRPP $A = 0.09$, $p < 0.01$) and change through time (MRPP $A = 0.24$, $p < 0.01$) (a). Short dashed lines represent summer months, whereas long dashed lines represent winter and spring months. NMDS axes correlate with the density of two numerically dominant species, *Baetis* and *Hydropsyche*, which make up 32 and 25% of the invertebrate assemblage, respectively (Table 3). *Hydropsyche* shows strong variation by reach and is more abundant in the unrestored reach (b). *Baetis* shows strong seasonal variation and is more abundant in winter/spring months than summer/fall months (c). The Pearson correlation coefficient (r) is reported for panels (b) and (c).

The grazing mayfly *Baetis* also tended to be less abundant in the restored reach ($F_{[1,19]} = 3.41$, $p = 0.08$). However, because the abundance of *Hydropsyche* declined in the restored reach to a much greater extent than the abundance of *Baetis*, proportional abundance shifted from dominance by the filter-feeding caddisfly in the unrestored reach to dominance by the grazing mayfly in the restored reach.

Experiment

To assess the role of two potential factors causing the change in invertebrate assemblage in the restored reach, we performed an experiment in which we manipulated the mobility and heterogeneity of substrates in factorial combination in the two study reaches. Total invertebrate abundance and biomass (Fig. 4a & 4b) were lower (Table 2) in treatments containing homogeneous substrates. Abundance declined nearly 50%, from $4,744 \pm 812$ individuals/m^2 in heterogeneous treatments to $2,551 \pm 392$ individuals/m^2 in homogeneous treatments. Biomass declined to an even greater extent, from 12.3 ± 3.1 g/m^2 in heterogeneous treatments to 4.25 ± 0.76 g/m^2 in homogeneous treatments (65%). Abundance and biomass also declined in treatments of increased substrate mobility (Fig. 4a & 4b), although these differences were not significant (Table 2) due to high variability among replicate experimental units.

In contrast to abundance and biomass, and contrary to the results of our monitoring efforts, neither species richness nor evenness differed among experimental treatments (Table 2; Fig. 4c & 4d). Experimental units placed in the restored reach

tended to have higher levels of richness than those in the unrestored reach (Table 2). Even so, most species present in a reach was found in each experimental unit, and there was no consistent difference in dominance among treatments (Fig. 4d). Ordination of invertebrate assemblages did, however, reveal more subtle shifts in invertebrate composition among treatments. Axes 1 and 2 of a community ordination explained 77% of variation in the dataset. With just one exception (mobility treatment, restored reach), community structure in experimental units containing homogeneous substrates shifted to the right of units containing heterogeneous substrates along NMDS Axis 1 toward communities that were more typical of those observed in our monitoring efforts in the restored reach (Fig. 5a). For all treatments of increased substrate mobility, invertebrate community structure in experimental units containing mobile substrates shifted above units containing non-mobile substrates along NMDS Axis 2, again, toward communities more typical of the restored reach. Together, these trends suggest that invertebrate assemblages in treatments of increased substrate mobility and decreased substrate heterogeneity were more similar to invertebrates found in the restored reach.

Shifts in invertebrate assemblages in the experimental treatments were once again driven by changes in abundance of the two dominant taxa—*Baetis* and *Hydropsyche*. Both the absolute (Table 3) and proportional (Fig. 5b) abundance of *Hydropsyche* decreased in treatments of increased substrate mobility. An indicator species analysis confirmed that *Hydropsyche* was positively associated with the no mobility
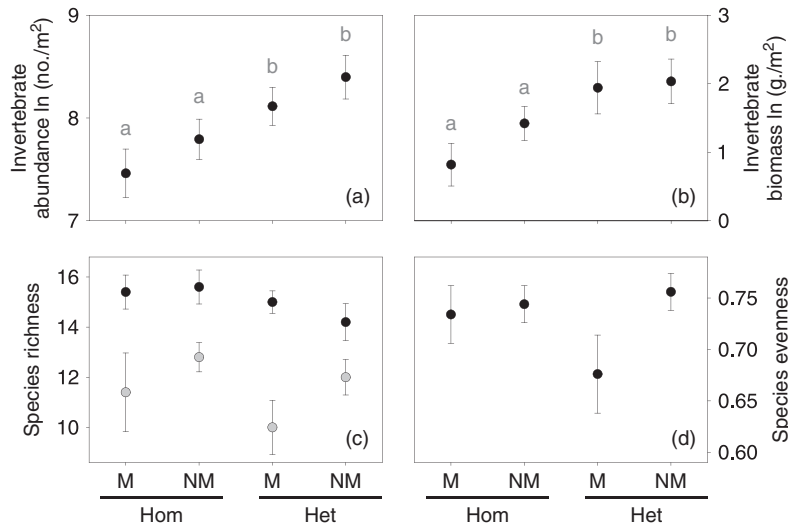
Figure 4. Community-level patterns from the in situ experiment showing the effects of heterogeneity and mobility on invertebrate assemblages. Values give the means ±1 SE for experimental units pooled from both reaches in panels a, b, and d, and means ±1 SE in the restored versus unrestored reach for panel c (note the significant effect of reach in Table 2). Invertebrate abundance (a) and biomass (b) are lower in treatments with homogeneous substrate sizes but do not respond to substrate mobility. Species richness (c) showed no response to either rock heterogeneity or mobility and only differed among reaches ($p < 0.01$, restored = black dots, unrestored = gray dots). Evenness (d) was not affected by any treatment. Statistically similar treatments are indicated by "a" and "b." Hom = homogeneous, Het = heterogeneous, NM = no mobility, and M = mobility treatments.

Table 2. Results from general linear models showing the effects of study reach, substrate heterogeneity, and substrate mobility on invertebrate abundance, biomass, and diversity in the in situ experiment.

Dependent Variable	df	F	p
Total abundance (ln no./m^2)			
Reach	1,35	3.55	0.07
Heterogeneity	1,35	9.55	<0.01
Mobility	1,35	2.53	0.12
Total biomass (ln g/m^2)			
Reach	1,35	0.92	0.34
Heterogeneity	1,35	3.87	0.06
Mobility	1,35	2.07	0.16
Species richness			
Reach	1,35	32.78	<0.01
Heterogeneity	1,35	2.53	0.12
Mobility	1,35	1.2	0.28
Species evenness			
Reach	1,35	1.21	0.28
Heterogeneity	1,35	0.75	0.39
Mobility	1,35	2.87	0.1

The most parsimonious models were selected by eliminating nonsignificant higher order interactions. Treatment means and standard errors are shown in Fig. 4.

treatments ($p < 0.01$). In contrast, the absolute (Table 3) and proportional (Fig. 5c) abundance of *Baetis* declined in homogeneous treatments. An indicator species analysis confirmed that *Baetis* ($p < 0.01$) was positively associated with treatments that contained heterogeneous substrates.

Discussion

The ecological consequences of large-scale channel reconstruction are poorly understood in river systems despite being

a widely used restoration technique to create suitable habitat for biota. Here, we have presented results from a case study of stream restoration and have shown that channel reconstruction and gravel augmentation lead to a reduction in total invertebrate abundance and biomass, an increase in taxonomic diversity, and a shift in the numerically dominant species. Most of the changes we observed in the restored reach were attributable to two numerically dominant taxa—*Hydropsyche* and *Baetis*. Densities of both taxa were lower in the restored reach compared with the unrestored, reference reach. However, larvae of the sessile, filter-feeding caddisfly *Hydropsyche* declined more in abundance than nymphs of the mobile, grazing mayfly *Baetis*. As a result, invertebrate assemblages shifted from dominance by filter-feeding caddisflies in the unrestored reach to dominance by grazing mayflies in the restored reach.

Our experiment was able to shed light on factors that potentially underlie selected changes in invertebrate assemblages. By simulating a decrease in the heterogeneity and increase in mobility of substrates, we were able to reproduce the observed decline in total invertebrate abundance and biomass and to shift invertebrate assemblages away from a composition similar to that of the unrestored reach toward a composition more comparable with the restored reach. Although increased bed mobility appeared to play a minimal role in reducing total invertebrate abundance and biomass, it did contribute significantly to altering invertebrate composition by shifting the dominant species. Although the numerically dominant *Baetis* was largely unaffected by the mobility treatment, densities of the subdominant *Hydropsyche* were substantially reduced by bed mobility. The lack of response by *Baetis* may simply be due to the unusually high mobility of this species and its abundance in the drift that allows it to quickly recolonize
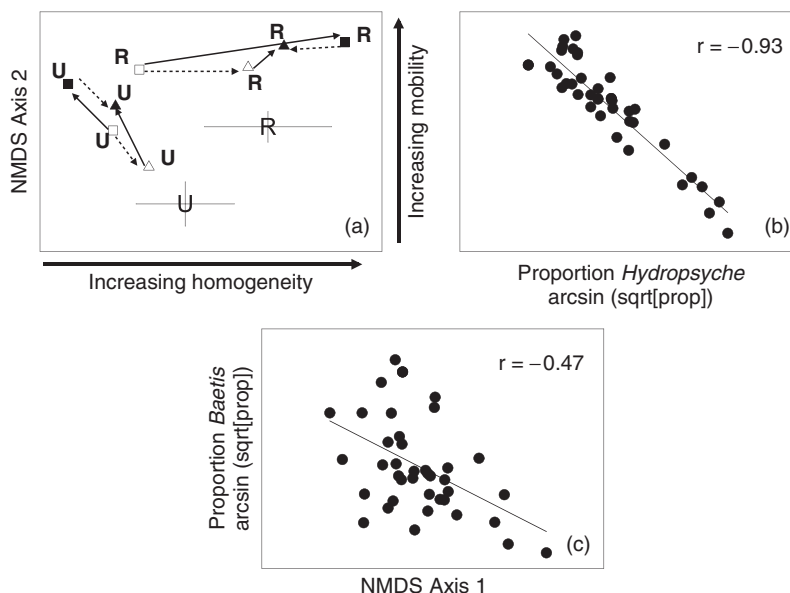
Figure 5. Results of multivariate community ordination (a) showing the impact of experimental treatments of rock heterogeneity and mobility on invertebrate assemblages. "U" and "R" represent mean ±1 SE ambient community structure in $n = 3$ unrestored and $n = 4$ restored riffles, respectively, on the sampling date (12 April 2008) of the experiment. Squares and triangles represent communities in experimental treatments of heterogeneous versus homogeneous rocks, respectively. Open and black shapes indicate non-mobile versus mobile treatments, respectively. Invertebrate communities in homogeneous treatments shift right of communities in heterogeneous treatments along NMDS Axis 1, as shown by dashed arrows pointing right from squares to triangles. Communities in treatments with mobile substrates shift above communities in treatments with non-mobile substrates along NMDS Axis 2, as indicated by solid arrows pointing up from white to black symbols. These trends were again largely driven by the two most dominant invertebrates, *Baetis* and *Hydropsyche*. The proportion of *Hydropsyche* decreased in treatments of increased substrate mobility (b). In contrast, the proportion of *Baetis* decreased in homogeneous treatments (c). The Pearson correlation coefficient (r) is reported for panels (b) and (c).

habitat (Mackay 1992). In contrast, net-spinning caddisflies are sessile invertebrates that are generally thought to require stable substrate to construct the catchnets with which they filter food (Mackay 1979; McCabe & Gotelli 2000). They have also been characterized by some as a "late successional" species, suggesting that they are relatively slow to colonize disturbed habitats compared with other invertebrates, but that once they do colonize, they competitively exclude other species that vie for space (Hemphill & Cooper 1983). Given these traits, as well as the results of our two studies, we strongly suspect that higher bed particle mobility in the restored reach is responsible for the reduced densities of *Hydropsyche*.

In contrast to the role of bed mobility, a reduction in substrate heterogeneity appeared to be primarily responsible for lower overall invertebrate abundance and biomass. This trend was mostly driven by a reduction in the densities of *Baetis* in the homogeneous substrate treatments. It is unclear to us why *Baetis* responded so strongly to homogenization of particle sizes. Prior research with stream invertebrates has shown that substrate heterogeneity can regulate invertebrate densities by any of three non-mutually exclusive mechanisms: (1) providing flow refugia during floods (Brown 2003), (2) providing refugia from predators (Diehl 1992; Power 1992), and (3) altering food sources, such as that occurs when algal growth is stimulated in environments that have heterogeneous flow (Downes et al. 1998; Cardinale et al. 2002). Any of these mechanisms could potentially apply to

Baetis. As one of the most mobile stream grazers, mayflies like *Baetis* are known to have high dispersal (Holomuzki & Biggs 2000) and refuge seeking (Brittain & Eikeland 1988) capability during high discharge events, as well as the tendency to seek out patches of high algal density (Kohler 1985). *Baetis* is also one of the most common prey items documented in studies of fish diets (Merz & Vanicek 1996). Further work is needed to determine why homogenization of substrates in restored streams reduces mayfly densities.

Although our experimental manipulations successfully mimicked declines in invertebrate abundance, biomass, and shifts in composition, they could not reproduce the observed increases in species richness and evenness in the restored reach. There are several possible reasons for this discrepancy; here we mention just two. First, our experiment suffers all of the same limitations of spatial scale as most in situ experiments do. The relatively small experimental units used in our study could have limited our ability to observe certain taxonomic groups, such as those with limited distributions or small population sizes. As such, we may have underestimated diversity. Second, for reasons already discussed in Methods section, the frequency of disturbance applied to the increased bed mobility treatment was greater than the typical bankfull discharge that occurs in this stream. As a result, organisms had only 4 weeks to colonize the experimental baskets between the final disturbance and the sampling date, which is less time than they typically have to recolonize the restored reach between the

Table 3. The mean density (no./m^2) ± 1 standard error of invertebrate taxa found in unrestored ($n = 3$) and restored ($n = 4$) riffles over 12 sampling dates.

| | Monitoring | | Experiment | | | |
| | | | Heterogeneous | | Homogeneous | |
Taxa	Unrestored Reach	Restored Reach	Non-mobile	Mobile	Non-mobile	Mobile
Hydropsyche	1,304 ± 1,080	482 ± 713	378 ± 338	109 ± 75	226 ± 219	67 ± 64
Baetis	1,198 ± 779	883 ± 733	1,690 ± 1,024	1,877 ± 1,595	902 ± 599	746 ± 454
Heptagenia	204 ± 183	570 ± 410	295 ± 231	185 ± 111	308 ± 307	283 ± 394
Chironomidae	244 ± 270	276 ± 267	809 ± 688	563 ± 389	351 ± 340	360 ± 526
Dugesia	151 ± 162	169 ± 118	151 ± 256	50 ± 82	121 ± 131	49 ± 36
Tricorythodes	33 ± 46	72 ± 74	889 ± 1,075	368 ± 423	358 ± 289	232 ± 173
Agathon	59 ± 89	21 ± 31	2 ± 7	5 ± 14	0	0.6 ± 1
Riffle beetle	9 ± 23	53 ± 76	119 ± 259	13 ± 29	11 ± 14	36 ± 57
Tubificidae	30 ± 66	43 ± 52	51 ± 104	88 ± 101	26 ± 26	13 ± 27
Culoptila	25 ± 100	33 ± 71	61 ± 110	102 ± 152	77 ± 101	48 ± 58
Corbicula	33 ± 46	11 ± 19	264 ± 166	93 ± 109	160 ± 123	124 ± 148
Simulium	29 ± 37	24 ± 28	184 ± 180	198 ± 79	55 ± 58	80 ± 74
Lumbricidae	9 ± 17	23 ± 51	349 ± 897	30 ± 33	32 ± 52	19 ± 26
Hyalella	7 ± 19	22 ± 27	44 ± 79	11 ± 15	9 ± 13	29 ± 79
Snail*	4 ± 9	22 ± 24	0.8 ± 2	11 ± 29	9 ± 19	35 ± 78
Asellus	2 ± 10	13 ± 33	21 ± 41	31 ± 77	111 ± 252	31 ± 60
Isoperla	12 ± 37	9 ± 24	52 ± 61	26 ± 43	31 ± 21	18 ± 23
Ceratopsyche	12 ± 70	0	0	0	0	0
Ceraclea	3 ± 15	7 ±18	40 ± 106	26 ± 27	23 ± 41	23 ± 53
Wormaldia	6 ± 16	2 ± 7	83 ± 104	35 ± 65	20 ± 28	25 ± 48
Acarina	5 ± 12	2 ± 8	6 ± 14	0	1 ± 4	2 ± 5
Anodonta	2 ± 7	0	0	0	0	0
Petrophila	2 ± 7	0	0	0	0	0
Rhizelmis	0	1 ± 9	0	0	0	0
Lineatipes	0	0.6 ± 4	0	0	0	0
Cleptelmis	0	0.3 ± 2	0	0	0	0
Glossosoma	0.08 ± 0.4	0.002 ± 0.12	0	0	0	2 ± 7
Hydaticus	0	0	4 ± 13	0	0	0
Limnophilidae	0	0	0	0	0	8 ± 27
Total	3,553 ± 1,595	2,874 ± 1,538	5,556 ± 4,376	3,841 ± 2,215	2,868 ± 1,718	2,233 ± 1,816

Densities in various treatment combinations of the in situ experiment are also shown. Sample sizes for the experiment were non-mobilized heterogeneous rocks ($n = 10$), mobilized heterogeneous rocks ($n = 9$), non-mobilized homogeneous rocks ($n = 10$) and mobilized homogeneous rocks ($n = 10$).
* Snail category includes both *Physa* and Planorbidae.

large fall and spring floods (although small portions of the bed do move almost daily, Fig. 1c). Again, this could potentially leads to an underestimate of diversity.

Implications for Fish

Attempts to restore stream ecosystems in the western United States seldom focus on invertebrate communities as the ultimate goal. Rather, the focus is typically on enhancement of threatened or endangered fish. In the Central Valley of California where our work was performed, the most common species of concern is Chinook salmon, and one of the more common restoration practices is to restructure channels and add gravel to a streambed in order to enhance spawning habitat for adult salmon. Our studies suggest that, regardless of whether restoration efforts enhance spawning habitat, those same efforts might have indirect and unintended consequences for other life-history stages.

The wholesale decline in the abundance and biomass of invertebrates that we documented in the restored reach has major implications for fish. It is widely recognized that the quantity of prey items and their carbon content limit the growth and survival of salmonids during the juvenile life-stage (Gibson 1993). Invertebrate abundance has also been shown to be a good predictor of Chinook feeding (Esteban & Marchetti 2004). Therefore, our findings that potential invertebrate prey items declined by 19% in the restored reach, and total invertebrate biomass declined by 62%, have major implications for how restoration practices might influence non-target life-stages of Chinook.

Our study also suggests that there might be more subtle effects of an altered food web on juvenile fish. Although juvenile salmon are sometimes described as opportunistic feeders (Sagar & Glova 1988; Merz & Vanicek 1996), limited evidence suggests that salmonids feed disproportionately on mayflies like *Baetis*, perhaps because mayflies tend to be disproportionately abundant in stream drift (Sagar & Glova 1988; Rader 1997). There is also some evidence that salmonids feed preferentially on large-bodied invertebrate prey like

Hydropsyche in spite of their low relative abundance in the drift (Rondorf et al. 1990; Amundsen et al. 2001). If juvenile Chinook do indeed exhibit preferential feeding, then much empirical and theoretical work suggests that the relative abundance of a preferred prey item will influence predator efficiency and food capture rates (MacArthur & Pianka 1966; Strauss 1979). As such, the shift in the relative abundance of species that we documented—from dominance by large-bodied *Hydropsyche* to dominance by the smaller, but more prone to drift *Baetis*—could also have important implications for fish growth and survival.

Comparison to Other Studies

Despite the wealth of information on the importance and role of substrate sizes and types on benthic species in rivers (Cummins & Lauf 1969; Rabeni & Minshall 1977; Mackay 1992), there is a paucity of information about how stream restoration practices that alter gravel substrates influence benthic food webs (but see Harrison et al. 2004; Sarriquet et al. 2007). Because of this, it is unclear whether the findings of our study are likely to be general and applicable to other streams or invertebrate communities. Within the Central Valley of California, we know of just one other study similar to ours, and it is noteworthy to mention that study found contrasting results. Although we found that abundance, biomass, and community composition were different in the restored site after gravel augmentation in the Merced River, Merz and Chan (2005) found that invertebrate density, biomass, and species richness in a restored site of the Mokolumne River were similar to that of an unrestored reference site within 4 weeks, and that density and biomass were higher in the restored site 1 year following gravel enhancement. Merz and Chan (2005) also found that, within 4 weeks, the abundance of both *Baetis* and *Hydropsyche* in the restored site was comparable with the unrestored reference site. Although we can only speculate as to why there might be differences between our study and theirs, one possibility is that the 4-week census by Merz and Chan detected transient colonization in the restored reach and did not allow enough time for a high flow events to influence species that are sensitive to disturbance or the natural sorting of particle sizes. Regardless, we wish to emphasize that the studies addressing how geomorphology impacts invertebrate at the base of food webs in restoration sites remains rare.

Conclusions

As a case study of restoration in a single river, our conclusions and inferences are inherently constrained. However, to the extent that our results are general, our study suggests that restoration by channel reconstruction and gravel augmentation can have unintended, indirect effects on non-target life-stages of focal species. In California where our work was performed, numerous restoration projects focus on creating adult spawning habitat by augmenting gravel beds, and here we have shown that those same projects can alter abundance, biomass, and composition of invertebrates that represent dominant prey items for fish. Future work must now address whether such shifts in invertebrate communities create more or less favorable conditions for the various life-stages of the focal species to better inform the management and rehabilitation of critical habitats that sustain biota.

Implications for Practice

- Our study illustrates that the widely used river restoration technique of gravel augmentation can drive shifts in invertebrate assemblages that compose the food-base available to fish.
- This indicates that restoration efforts may have unintended, indirect consequences for non-target life-stages of focal species, such as juvenile salmon.
- To understand how effective current restoration efforts are, future work must establish if and how these projects provide conditions that are favorable for the various life-stages that influence population sizes of the focal species.

LITERATURE CITED

Amundsen, P., H. Gabler, and L. S. Riise. 2001. Intraspecific food resource partitioning in Atlantic salmon (*Salmo salar*) parr in a subarctic river. Aquatic Living Resources **14**:257–265.

Beisel, J. N., P. Usseglio-Polatera, and J. C. Moreteau. 2000. The spatial heterogeneity of a river bottom: a key factor determining macroinvertebrate communities. Hydrobiologia **422**:163–171.

Bernhardt, E. S., M. A. Palmer, J. D. Allan, G. Alexander, K. Barnas, S. Brooks, et al. 2005. Ecology: synthesizing U.S. river restoration efforts. Science **308**:636–637.

Brittain, J. E., and T. J. Eikeland. 1988. Invertebrate drift—a review. Hydrobiologia **166**:77–93.

Brooks, S. S., M. A. Palmer, B. J. Cardinale, C. M. Swan, and S. Ribblett. 2002. Assessing stream ecosystem rehabilitation: limitations of community structure data. Restoration Ecology **10**:156–168.

Brown, B. L. 2003. Spatial heterogeneity reduces temporal variability in stream insect communities. Ecology Letters **6**:316–325.

Buffington, J. M., and D. R. Montgomery. 1997. A systematic analysis of eight decades of incipient motion studies, with special reference to gravel-bedded rivers. Water Resources Research **33**:1993–2029.

Cardinale, B. J., M. A. Palmer, C. M. Swan, S. Brooks, and N. L. Poff. 2002. The influence of substrate heterogeneity on biofilm metabolism in a stream ecosystem. Ecology **83**:412–422.

CDWR (California Department of Water Resources). 2005. The Merced River Salmon habitat enhancement project: Robinson reach phase III. San Joaquin District, Fresno, California. 159 p.

Chapman, D. W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Transactions of the American Fisheries Society **117**:1–21.

Cummins, K. W., and G. H. Lauf. 1969. The influence of substrate particle size on the microdistrubution of stream macrobenthos. Hydrobiologia **34:**145–181.

Death, R.G., and M. J. Winterbourn. 1995. Diversity patterns in stream benthicinvertebrate communities: the influence of habitat stability. Ecology **76:**1446–1460.

Diehl, S. 1992. Fish predation and benthic community structure—the role of omnivory and habitat complexity. Ecology **73:**1646–1661.

Dobson, A. P., A. D. Bradshaw, and A. J. M. Baker. 1997. Hopes for the future: restoration ecology and conservation biology. Science **277:**515–522.

Downes, B. J., P. S. Lake, E. S. G. Schreiber, and A. Glaister. 1998. Habitat structure and regulation of local species diversity in a stony, upland stream. Ecological Monographs **68:**237–257.

Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs **67:**345–366.

Esteban, E. M., and M. P. Marchetti. 2004. What's on the menu? Evaluating a food availability model with young-of-the-year Chinook salmon in the Feather River, California. Transactions of the American Fisheries Society **133:**777–788.

Fisher, S. G., L. J. Gray, N. B. Grimm, and D. E. Busch. 1982. Temporal succession in adesert stream following flooding. Ecological Monographs **32:**93–110.

Gibson, R. J. 1993. The Atlantic salmon in fresh water: spawning, rearing and production. Reviews in Fish Biology and Fisheries **3:**39–73.

Gotelli, N. J., and G. L. Entsminger. 2008. EcoSim: null models software for ecology. Version 7. Acquired Intelligence, Inc. & Kesey-Bear, Jericho, Vermont 05465. http://garyentsminger.com/ecosim.htm.

Harrison, L. R., C. J. Legleiter, M. A. Wydzga and T. Dunne (in revision). Channel dynamics and habitat development in a meandering, gravel-bed river. Water Resources Research.

Harrison, S. S. C., J. L. Pretty, D. Shepherd, A. G. Hildrew, C. Smith, and R. D. Hey. 2004. The effect of instream rehabilitation structures on macroinvertebrates in lowland rivers. Journal of Applied Ecology **41:**1140–1154.

Hemphill, N., and S. D. Cooper. 1983. The effect of physical disturbance on the relative abundances on two filter-feeding insects in a small stream. Oecologia **58:**378–382.

Holomuzki, J., and B. Biggs. 2000. Taxon-specific responses to high-flow disturbance in streams: implications for population persistence. Journal of the North American Benthological Society **19:**670–679.

Kohler, S. L. 1985. Identification of stream drift mechanisms: an experimental and observational approach. Ecology **66:**1749–1761.

Kondolf, G. M., and W. V. G. Mathews. 1993. Management of coarse sediment in regulated rivers in California. Report Number 80, University of California Water Resources Center, Riverside.

Lamberti, G. A., and V. H. Resh. 1979. Substrate relationships, spatial distribution patterns, and sampling variability in a stream Caddisfly population. Environmental Entomology **8:**561–567.

Levin, S. A. 1976. Population dynamic models in heterogeneous environments. Annual Review of Ecology and Systematics **7:**287–310.

MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. The American Naturalist **100:**603.

Mackay, R. J. 1979. Life-history patterns of some species of *Hydropsyche* (Trichoptera: Hydropsychidae) in southern Ontario. Canadian Journal of Zoology **57:**963–976.

Mackay, R. J. 1992. Colonization by lotic macroinvertebrates—a review of processes and patterns. Canadian Journal of Fisheries and Aquatic Sciences **49:**617–628.

Matthaei, C. D., C. J. Arbuckle, and C. R. Townsend. 2000. Stable surface stones as refugia for invertebrates during disturbance in a New Zealand stream. Journal of North American Benthological Society **19:**82–93.

McCabe, D. J., and N. J. Gotelli. 2000. Effects of disturbance frequency, intensity, and area on assemblages of stream macroinvertebrates. Oecologia **124:**270–279.

McCune, B., and M. J. Mefford. 2006. PC-ORD v5. Multivariate Analysis of Ecological Data. MJM Software, Gleneden Beach, Oregon.

Merritt, K. W., and R. W. Cummins. editors. 1996. An introduction to the aquatic insects of North America. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Merz, J. E., and L. K. O. Chan. 2005. Effects of gravel augmentation on macroinvertebrate assemblages in a regulated California river. River Research and Applications **21:**61–74.

Merz, J. E., and C. D. Vanicek. 1996. Comparative feeding habits of juvenile Chinook salmon, steelhead, and Sacramento squawfish in the lower American River, California. California Fish and Game **82:**149–159.

Moyle, P. B. 1994. The decline of anadromous fishes in California. Conservation Biology **8:**869–870.

Pacala, S. W., and J. Roughgarden. 1982. Spatial heterogeneity and interspecific competition. Theoretical Population Biology **121:**92–113.

Palmer, M. A., R. F. Ambrose, and N. L. Poff. 1997. Ecological Theory and Community Restoration Ecology. Restoration Ecology **5:**291–300.

Palmer, M. A., E. S. Bernhardt, J. D. Allan, P. S. Lake, G. Alexander, S. Brooks, et al. 2005. Standards for ecologically successful river restoration. Journal of Applied Ecology **42:**208–217.

PFMC (Pacific Fisheries Management Council). 2008. Record low salmon fisheries adopted. (Available from www.pcouncil.org/newsreleases/PFMC_FINAL_PressRel.pdf) accessed 1 January 2009.

Power, M. E. 1992. Habitat heterogeneity and the functional-significance of fish in river food webs. Ecology **73:**1675–1688.

Rabeni, C. F., and G. W. Minshall. 1977. Factors affecting the microdistribution of stream benthic insects. Oikos **29:**33–43.

Rader, R. B. 1997. A functional classification of the drift: traits that influence invertebrate availability to salmonids. Canadian Journal of Fisheries and Aquatic Sciences **54:**1211–1234.

Rempel, L. L., J. S. Richardson, and M. C. Healey. 1999. Flow refugia for benthic macroinvertebrates during flooding of a large river. Journal of the North American Benthological Society **18:**34–48.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society **7:**433–455.

Richards, C., G. E. Host, and J. W. Arthur. 1993. Identification of predominant environmental factors structuring stream macroinvertebrate communities within a large agricultural catchment. Freshwater Biology **29:**285–294.

Rondorf, D. W., G. A. Gray, and R. B. Fairley. 1990. Feeding ecology of subyearling Chinook Salmon in Riverine and reservoir habitats of the Columbia River. Transactions of the American Fisheries Society **119:**16–24.

Sagar, P. M., and G. J. Glova. 1988. Diel feeding periodicity, daily ration and prey selection of a riverine population of juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). Journal of Fish Biology **33:**643–653.

Sarriquet, P. E., P. Bordenave, and P. Marmonier. 2007. Effects of bottom sediment restoration on interstitial habitat characteristics and benthic macroinvertebrate assemblages in a headwater stream. River Research and Applications **23:**815–828.

Shields, A. 1936. Anwendung der Aehnlichkeitsmechanik und der Turbulenzforschung die Geschiebebewegung. Mitt. Preuss, Versuchsanst, Wasserbau Schiffbau 26.

Sørensen, T. J. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analysis of the vegetation of the Danish Commons. Biologiske Skrifter **5:**1–34.

Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology **60:**1225–1239.

Stewart-Oaten, A., W. W. Murdoch, and K. R. Parker. 1986. Environmental impact assessment: "pseudoreplication" in time? Ecology **67:**929–940.

Strauss, R. 1979. Reliability estimates for Ivlev electivity index, the forage ratio, and a proposed linear index of food selection. Transactions of the American Fisheries Society **108:**344–352.

Trush, W. J., S. M. McBain, and L. B. Leopold. 2000. Attributes of an alluvial river and their relation to water policy and management. Proceedings of the National Academy of Sciences **97:**11858–11863.

Vinson, M. R., and C. P. Hawkins. 1998. Biodiversity of stream insects: variation at local, basin, and regional scales. Annual Review of Entomology **43:**271–293.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human Domination of Earth's Ecosystems. Science **277:**494–497.

Yoshiyama, R. M., E. R. Gerstung, F. W. Fisher, and P. B. Moyle. 2001. Historical and present distribution of Chinook Salmon in the central valley drainage of California. Fish Bulletin **179:**71–176.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Habitat conditions are similar between the two study reaches. Temperature values are shown as mean daily temperature (minimum, maximum) from September 2008 until April 2009 in riffles for the restored reach ($n = 3$) and unrestored reach ($n = 2$). Other factors are shown as mean values (with values from each riffle in parentheses) in the restored ($n = 2$) and unrestored ($n = 2$) reaches.

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.