EFFECTS OF GRAVEL AUGMENTATION ON MACROINVERTEBRATE ASSEMBLAGES IN A REGULATED CALIFORNIA RIVER

JOSEPH E. MERZ[a,b]* and LEIGH K. OCHIKUBO CHAN[b]

[a] *Wildlife, Fish, and Conservation Biology Department, University of California, One Shields Avenue, Davis, CA 95616-8751, USA*
[b] *East Bay Municipal Utility District, 1 Winemasters Way, Lodi, CA 95240, USA*

ABSTRACT

Enhancement projects within anadromous salmonid rivers of California have increased in recent years. Much of this work is intended as mitigation in regulated streams where salmon and steelhead spawning habitat is inaccessible or degraded due to dams, water diversions and channelization. Little research has been done to assess the benefits of spawning habitat enhancement to stream organisms other than salmon. We monitored benthic macroinvertebrates at seven spawning gravel augmentation sites in the lower Mokelumne River, a regulated stream in the Central Valley of California. Placement of cleaned floodplain gravel decreased depths and increased stream velocities. Benthic organisms colonized new gravels quickly, equalling densities and biomass of unenhanced spawning sites within 4 weeks. Macroinvertebrate species richness equalled that of unenhanced sites within 4 weeks and diversity within 2 weeks. Standing crop, as indicated by densities and dry biomass, was significantly higher in enhancement sites after 12 weeks than in unenhanced sites and remained so over the following 10 weeks. Although mobile collector/browsers initially dominated new gravels, sedentary collectors were the most common feeding category after 4 weeks, similar to unenhanced sites. These data suggest that cleaned gravels from adjacent floodplain materials, used to enhance salmonid spawning sites, are quickly incorporated into the stream ecosystem, benefiting benthic macroinvertebrate densities and dry biomass. Copyright © 2005 John Wiley & Sons, Ltd.

KEY WORDS: river enhancement; macroinvertebrates; salmon; spawning; gravel; biomass; species diversity; physical habitat

INTRODUCTION

Alluvial streams in semi-arid climates may transport large amounts of bed material, especially during rain and snowmelt pulses (Andrews and Nankervis, 1995). Adaptations of biota to these 'pulses' include the regeneration of riparian plant species (Mahoney and Rood, 1998), seasonal migrations and life stages of numerous native fish species (Sommer *et al.*, 2001; Bennett *et al.*, 2002) and diversity and development of benthic macroinvertebrate communities (Townsend *et al.*, 1997).

Damming, regulation, levee construction, water diversion and mining have disrupted natural sediment transport mechanisms, including timing, frequency, agitation and cleansing, processes important to the flora and fauna of riverine systems (Collins and Dunne, 1989; Kondolf, 1997). Sediment-starved rivers are prone to channel bed and bank erosion, channel incision, coarsening bed material and reduced habitat heterogeneity (Brooks and Boulton, 1991; Kondolf, 1997). Stream channelization may further exacerbate these problems, decreasing abundance and diversity of riverine species (Negishi *et al.*, 2002).

RESTORATION EFFORTS IN SEDIMENT-STARVED SYSTEMS

Numerous techniques have been used in restoration and enhancement projects in an attempt to ameliorate these impacts. Wheaton *et al.* (in press) segregate improvement projects into three sometimes-overlapping categories: (1) gravel augmentation, (2) structural improvements and (3) habitat enhancement. The most common

---

*Correspondence to: Joseph E. Merz, Wildlife, Fish, and Conservation Biology Department, University of California, One Shields Avenue, Davis, CA 95616-8751, USA. E-mail: jmerz@ebmud.com

improvement projects in North America have been structural, including current deflectors, overpour structures, bank cover and boulder placements (Gore *et al.*, 1998). These projects can be successful. For example, Fuselier and Edds (1995) showed that an artificial riffle, constructed in an area of previously dredged gravel, improved habitat for the Neosho madtom (*Noturus placidus*). The artificial riffle had similar fish species diversity and richness to natural riffles in the Cottonwood River, Kansas, after 1 year. Gravel augmentation has received increasing attention as a restoration tool to improve salmonid spawning habitat in sediment-starved systems, especially on regulated systems (Scrutin *et al.*, 1997; Nakamura, 1999). In California alone, gravel augmentation was taking place on more than 13 dammed Sierra Nevada rivers beginning as early as 1979 (Kondolf and Mathews, 1993). Little work has been done to assess whether gravel augmentation actually improves salmonid spawning habitat and even less study has centred on the effects of gravel augmentation on associated organisms. For instance, many lotic macroinvertebrate species are found in riffle areas with streambed substrate of gravel or rubble which is the same habitat utilized by many anadromous salmonid species for spawning (Platts *et al.*, 1983; Mangum, 1986; Groot and Margolis, 1991). This is surprising considering the importance of benthic macroinvertebrates to the ecology of lotic systems (Gore, 1985; Hershey *et al.*, 1993; Hamilton and Barclay, 1998; Hocking and Reimchen, 2002) and the significant impacts river regulation has on these communities.

The use of benthic macroinvertebrates to assess enhancement or restoration projects is relatively new (Ebrahimnezhad and Harper, 1997; Gørtz, 1998; Muotka *et al.*, 2002). Results of such studies have been variable due to study length and project size (Tikkanen *et al.*, 1994; Laasonen *et al.*, 1998). Aquatic macroinvertebrates, especially insects, are often used in water quality assessment due to their ubiquity, sedentary nature and length of life cycles. These traits make them useful indicators of temporal and spatial changes in aquatic habitats (Rosenberg and Resh, 1993, 1996). Furthermore, colonization rates and eventual macroinvertebrate community structure on new substrate may demonstrate how well 'rehabilitated' sites are incorporated into the river system.

Macroinvertebrate colonization of artificial substrates in lentic and lotic environments has been well discussed in the literature (Lake and Doeg, 1985; Brooks and Boulton, 1991; Benoit *et al.*, 1998; Quinn *et al.*, 1998). Mackay (1992) describes processes and patterns of lotic macroinvertebrate colonization, and Ebrahimnezhad and Harper (1997) have assessed the biological effectiveness of riffle construction for the benthic community in an artificial channel. Assessment of habitat improvement projects implies that we know what should be measured to evaluate success. According to Palmer *et al.* (1997), from a community ecology perspective, appropriate structural endpoints include measuring species richness of focal groups or entire assemblages. Functional restoration endpoints, in the strictest sense, refer to process measurements such as primary or secondary production, and the measurement of trophic levels and their connectiveness, functional groups, desired community structure and careful consideration of community level attributes, not just a focus on single species or clusters of 'desirable' species (Palmer *et al.*, 1997; Maddock, 1999). Colonization of enhanced or restored stream channels by aquatic communities has not been well documented, nor are the patterns of colonization well understood.

This paper examines the influence of salmonid spawning gravel augmentation on colonization and development of the benthic macroinvertebrate community of a regulated California Central Valley river. Specifically, we test the hypothesis that gravel augmentation will influence the density, biomass, species richness, diversity and evenness of benthic macroinvertebrates within the Chinook salmon spawning reaches of the regulated lower Mokelumne River.

STUDY SITE

Mokelumne River System

The Mokelumne River, California, drains approximately 1624 km^2 of the central Sierra Nevada. The lower Mokelumne River (LMR) includes approximately 54 km of regulated river between Camanche Dam, a complete barrier to anadromous fish, and the Sacramento–San Joaquin Delta (Figure 1). The river between Camanche Dam and Lake Lodi, a seasonal reservoir with a fish passage facility, is characterized by alternating bar complex and flatwater habitats, with a gradient of approximately 0.17 m km^{-1}. Similar to many other Central Valley rivers, the Mokelumne River has been affected by numerous human influences including 16 major water projects and instream gravel and gold mining (CDC, 1988; Kattelmann, 1996). Tailings from abandoned gold dredging operations are frequent along the upper one-third of the LMR. While many of the tailings are isolated from the river by
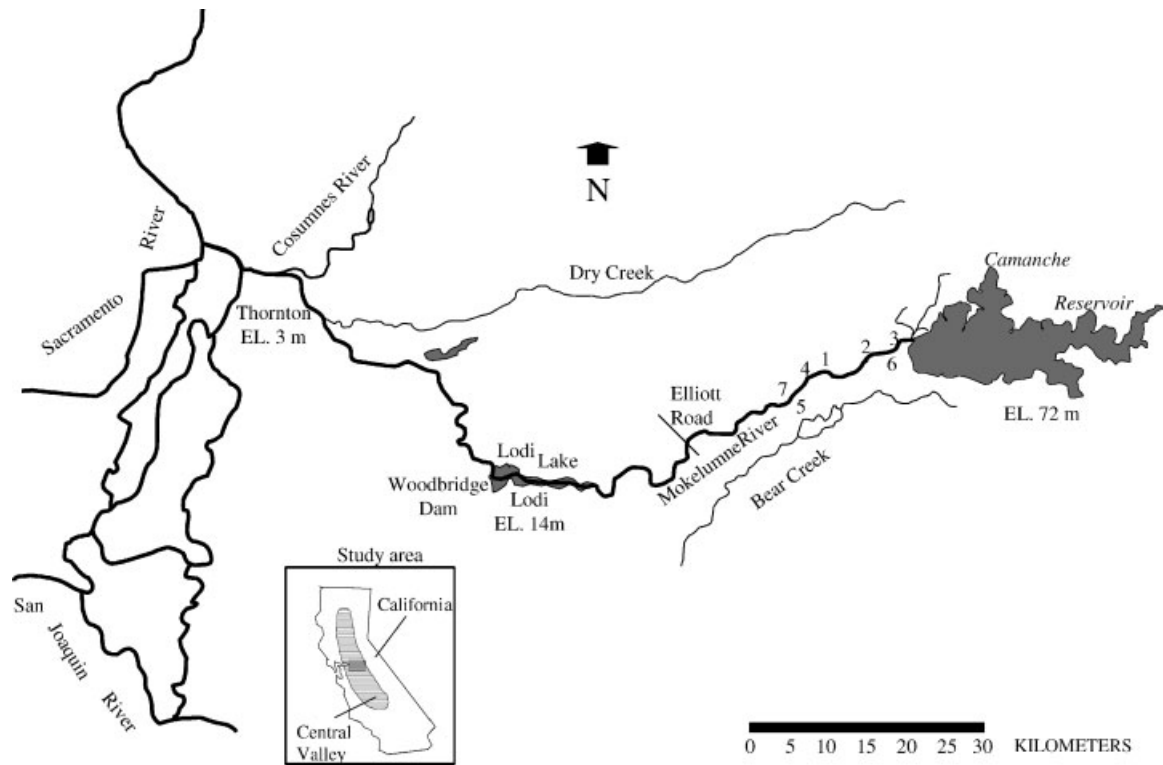
Figure 1. Location of the seven macroinvertebrate sampling sites within Chinook salmon spawning gravel enhancement locations on the lower Mokelumne River (California), and their spatial relationship to Camanche and Woodbridge dams

berms and levees, several large pits from gold and gravel dredging are now incorporated into the main river channel. Leveed banks and regulated flow greatly reduce lateral scour within this section of river, further impacting bedload recruitment.

At least 35 fish species occur in the LMR including two native anadromous salmonids, steelhead (*Oncorhynchus mykiss*) and fall-run Chinook salmon (*O. tschawytscha*) (Merz, 2002). It has been estimated that approximately 80% of historical Mokelumne River anadromous salmonid spawning habitat is now inaccessible due to construction of Camanche Dam. The quantity and quality of remaining habitat limits salmonid production (Menchen, 1961; FERC, 1998). Natural salmon and steelhead spawning now occurs within the upper 16 km of the LMR between Camanche Dam and Elliott Road (Figure 1). Both populations are supplemented with fish from the Mokelumne River Hatchery (local fish), the Feather River Hatchery and Nimbus Hatchery (American River). Mean annual discharge for the 25 years prior to this study was $20.3 \, \text{m}^3 \, \text{s}^{-1}$ (minimum: $0.7 \, \text{m}^3 \, \text{s}^{-1}$; maximum: $162.8 \, \text{m}^3 \, \text{s}^{-1}$). Detailed information on the lower Mokelumne River and its salmonid populations is also provided in Pasternack *et al.* (2003) and Merz and Setka (in press).

Gravel augmentation

Since 1990, East Bay Municipal Utility District, owner and operator of Camanche Dam, has performed annual Chinook salmon spawning enhancement projects in the LMR, including gravel augmentation to improve spawning habitat. These projects typically consist of placing approximately $380–1200 \, \text{m}^3$ of washed river rock (25–150 mm diameter) in berms and staggered gravel bar configurations. Site locations are selected within the spawning reach of fall-run Chinook salmon with easy access by roads for gravel-placing equipment. According to Merz and Setka (in press) historic aerial photographs (1933–1963) are used to select sites of previously shallow gravel that have been mined for gold or gravel between 1952 and 1964. Clean river gravel is placed by dump truck and rubber-tyre

Before gravel placement

August 1999

After gravel placement   ⟵ Mokelumne River Flow

September 1999

15 m

N

25   28
Elevation (m) above mean sea level

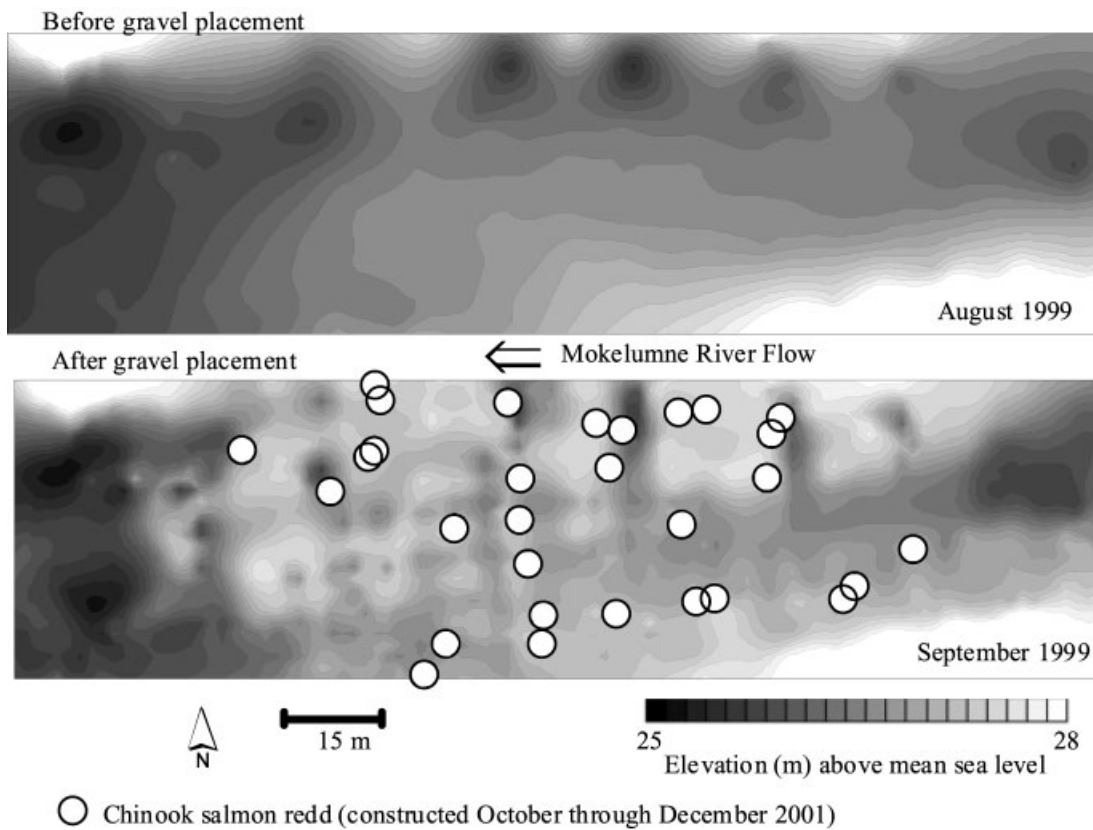○ Chinook salmon redd (constructed October through December 2001)

Figure 2. Chinook salmon spawning gravel enhancement site at Rkm 102.6 on the lower Mokelumne River. Increased elevation between August and September 1999 indicates gravel placement locations

loader in berm and staggered toe-bar configurations along each enhancement site. Configurations are chosen as a means to enhance Chinook salmon spawning conditions by reducing depth, increasing velocities, and promoting exchanges of water between the stream and the interstices of the gravel. Gravel placement is carried out between 15 August and 15 September of each year to avoid impacts on fish migration and spawning. Sites are typically 30 m wide by 65 m long (each site corresponds in size to 1–2% of remaining Chinook salmon spawning habitat) with an average depth of 0.4 m for placed gravels. Chinook salmon typically begin spawning in the new gravels within 3 months of gravel placement (Figure 2). Steelhead are uncommon. Preliminary assessment of these sites indicates that the projects increase intergravel permeability and dissolved oxygen and decrease intergravel temperatures in most situations (Merz and Setka, in press). Up to 49% of in-river Chinook salmon spawning now occurs within LMR enhancement sites (Setka, 2001).

METHODS

Channel topography and physical measurements

Topographic channel surveys of the enhancement sites before and after gravel placement were made with a Trimble 4000 GPS receiver, Leica T-1600 theodolite, DI-1600 electronic distance meter, and NA-2002 electronic level to record 2000–2800 individual reference points (latitude, longitude, elevation). Point spacing was quasi-systematic and stratified by grade-breaks and channel topography as opposed to a uniform grid (Brasington et al., 2000). Surveys were performed in early August, before gravel placement and again in late September, after gravel placement.

Depth (D) and water velocity (at $0.6 \times D$) were measured prior to and immediately after gravel placement using a Marsh-McBirney, Inc. Flo-Mate model 2000 portable flowmeter. Measurements were recorded every 60 cm at five evenly spaced transects within each site.

During September–January each year, salmonid spawning surveys were conducted weekly along the 16-km spawning reach below Camanche Dam. Redd locations were recorded using a hand-held Global Positioning System (GPS) unit (Trimble Pro XR) and a laser range finder (Atlanta Advantage). Survey data were downloaded to an American Standard Code for Information Interchange (ASCII) file and translated to the grid-based graphics program, Surfer® (Golden Software, Inc.). Reference points were used to construct digital terrain models and contour maps of sites before and after gravel placement with an overlay of salmon redds (Figure 2).

Substrate size

Newly placed gravel came from an open pit, dry quarry approximately 0.4 km south of the river channel. Therefore, new gravel was void of benthic organisms at time of placement (Week 0). Wolman pebble counts were conducted at three randomly selected transects (100 samples per transect) at each site prior to and immediately after gravel placement following the methods of Bauer and Burton (1993). Substrate from pebble counts was categorized into twelve sizes: <0.80, 0.80, 1.60, 2.22, 3.18, 4.45, 6.35, 8.90, 12.70, 17.78, 25.40, and >25.40 cm (Pasternack *et al.*, 2003). Cumulative percentages of each class were calculated.

Macroinvertebrate collection

Benthic macroinvertebrate collection was performed at seven spawning gravel enhancement sites along the LMR from 1996 to 2000. Benthic macroinvertebrates were collected with a 330 mm i.d. $\times$ 400 mm high, stainless steel 363 μm Nitex Hess Stream Sampler (bottom open area $= 0.086\,\mathrm{m}^2$) with an attached 368 μm dolphin bucket. Samples were taken to c. 15 cm depth within the substrate. Macroinvertebrates were collected both prior to and following gravel enhancement at all seven sites. Collections of benthic macroinvertebrates were made at four random points within a site in both pre- or unenhanced gravel and enhanced gravel areas. Pre-enhancement macroinvertebrate collection (Week 0) occurred approximately one week prior to gravel placement. Collected samples were placed in 500 ml Nalgene bottles in 95% ethyl alcohol. In order to maximize sampling efficiency, all samples were taken in riffle/run habitats with substrates dominated by gravel, in depths less than 60 cm and velocities between 0.25 and $1.00\,\mathrm{m\,s}^{-1}$, typical of Chinook salmon spawning ranges (Healey, 1991; Allen and Hassler, 1986).

Following gravel placement, macroinvertebrate samples were collected every 2 weeks to assess rates of colonization and changes in biomass and community structure based on colonization rates of previous studies (Waters, 1964; Shaw and Minshall, 1980). Samples were collected until flows became too high to wade the channel (typically late mid-January to July). In several instances, unenhanced substrate was slowly covered by scoured new material, ending comparative assessment. Dates of completed gravel placement and benthic sampling are provided in Table I.

Samples were transported to the laboratory and hand sorted using a $60 \times$ dissecting scope. When possible, organisms were identified to species. If taxa could not be identified to species, they were differentiated into apparent morphospecies. Size class (<2, 2–7, 8–13, 14–20, >20 mm) and life stage (larva/nymph, pupa and adult)

Table I. Date of gravel placement and benthic sampling at seven Chinook salmon spawning gravel enhancement sites in the lower Mokelumne River, California

Site	Completed gravel placement date	Date of first paired benthic sample (Week 2)	Date of last paired benthic sample
1	2 September 1996	16 September 1996	3 February 1997
2	2 September 1996	16 September 1996	21 January 1997
3	1 September 1997	23 September 1997	22 December 1998
4	1 September 1997	23 September 1997	22 December 1998
5	11 September 1998	29 September 1998	29 January 1999
6	9 September 1999	22 September 1999	27 January 2000
7	31 August 2000	13 September 2000	27 December 2000

were determined for each individual. Organisms were grouped into functional feeding categories following Merritt and Cummins (1996), Wiggins (1998), and Pennak (1989).

Dry biomass of samples was determined by oven drying samples of each taxonomic group (order or family) in representative life stage and size classes at 70°C for 24 hours to constant weight (Bowen, 1983). Samples were then weighed to the nearest 0.0001 gram. For extremely small organisms (<0.0001 g), groups of up to 20 individuals of the same life stage and size class were combined, and an average dry weight for that organism was calculated (Merz, 2002). The resulting average weights were multiplied by the count of that particular taxon present in a given sample to obtain a dry biomass measurement.

Data analyses

Structure and function of the benthic communities at each site were evaluated using density (no. m^{-2}), dry biomass (g density), taxa richness, Shannon's diversity (H) and evenness (J) and relative proportion of functional feeding guilds. We used Morisita's index (C) as described by Horn (1966) to analyse similarity of benthic communities from enhanced and unenhanced gravel sites, where a value of 0 indicates no species in common and a value of 1.0 indicates identical populations. We used a paired t-test to compare depths and velocities of each site before and after gravel placement. Differences in macroinvertebrate densities, dry biomass, species richness, diversity and evenness between enhanced and unenhanced gravel were examined using repeated measures ANOVA. We compared functional feeding categories between enhanced and unenhanced gravels by chi-squared.

RESULTS

Habitat configurations: channel depths, velocities and cumulative grain size distribution

A portion of the channel bed of seven sites was covered with up to 2.1 m of clean, quarry gravel, significantly increasing average bed elevation over each site by 0.17 m ($t = -1.90$, df = 317, $p < 0.001$). Gravel was typically applied in shallow bars, perpendicular to channel flow, providing a series of gravel deflectors throughout each site (e.g. Figure 2). These bars directed portions of the flow across veneers of new gravel, significantly increasing velocities throughout each site ($t = -10.98$; df = 103; $p < 0.001$). All seven sites attracted spawning Chinook salmon (Figure 2). Overall surface bed material had fewer fines (<8 mm) after gravel placement at each site (Figure 3).

Community structure

A total of 59 677 individuals representing 58 taxa was collected over the 5-year period. Colonization of new gravel gradually occurred over several weeks (Figure 4). There were no differences between mean macroinvertebrate densities on enhanced and unenhanced gravel from all seven sites by Week 6 ($F = 0.536$; df = 10; $p = 0.481$) and significantly greater densities on enhanced gravel by Week 10 ($F = 5.137$; df = 13; $p = 0.041$). Densities
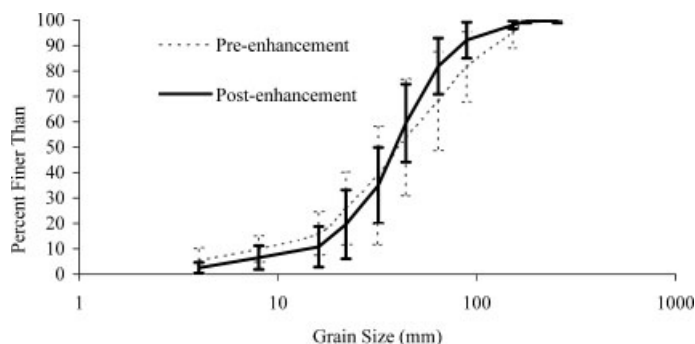

Figure 3.   Cumulative grain-size distributions for surface pebble counts taken before and after gravel augmentation at seven Chinook salmon spawning habitat enhancement sites in the lower Mokelumne River, California (1996–2000). Bars indicate one standard deviation
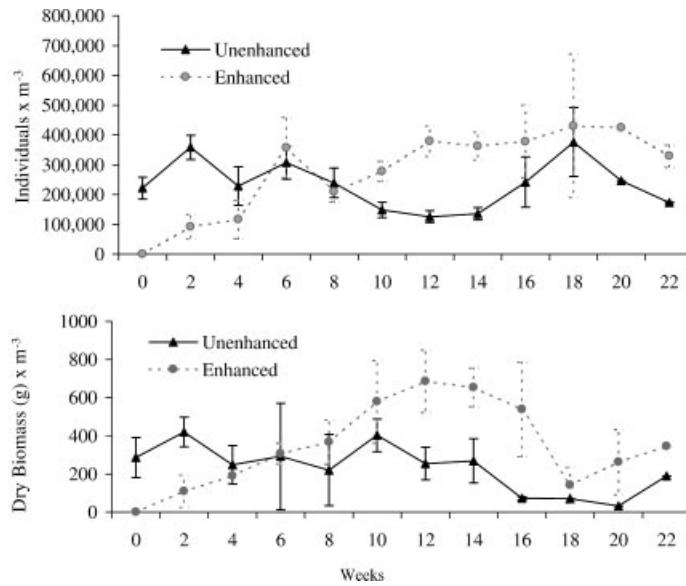
Figure 4. Total density and dry biomass of macroinvertebrates (mean ± standard error) at seven Chinook salmon spawning gravel enhancement sites

peaked at Week 6 and again at Week 18 in the enhancement gravels. Patterns for dry biomass were similar with average dry biomass significantly higher on the new gravel after Week 6 ($F = 6.940$; df $= 10$; $p = 0.025$). Peak biomass occurred at Week 12 in the enhancement gravels.

Taxa richness increased on the enhancement gravel gradually over the first 6 weeks with greatest change between the first and second week (Figure 5). Species richness on enhancement gravel peaked at Week 6 and again during Week 18. Overall species richness on enhancement gravel was not significantly different from unenhanced gravel by Week 6 ($F = 1.576$; df $= 10$; $p = 0.238$) and remained similar over the following 16 weeks ($p > 0.333$).

Shannon diversity (H) and Shannon evenness (J) in enhancement gravel both increased rapidly over the first 2 weeks (Figure 6). Enhanced and unenhanced gravel were not significantly different by Week 2 for both diversity ($F = 0.041$; df $= 12$; $p = 0.843$) and evenness ($F = 0.582$; df $= 12$; $p = 0.460$). Greatest evenness was observed in enhancement gravels at Week 2. Overlap in species composition of enhanced and unenhanced gravel was greatest during Week 16.

We found significant differences in mean densities of five of the ten most abundant taxa in the new gravel by Week 12 (Figure 7). Greatest differences were observed for *Baetis tricaudata* and *Hydropsyche californica*.

Functional feeding groups

Unenhanced gravels were dominated by sedentary collector/filterers, predominantly *H. californica*, *Simulium* sp. and *Cricotopus* sp. (35–52%) (Figure 8). Mobile collector/browsers, primarily *B. tricaudatus* and *Acentrella insignificans*, were the most common invertebrates in enhanced gravels during the first sampling period (Week 2: 37%). Feeding category distribution was different between enhanced and unenhanced gravel at this time ($G^2 = 27.4$; df $= 6$; $P < 0.001$). However, feeding categories were independent of gravel enhancement by Week 4 ($G^2 = 5.9$; df $= 6$; $P < 0.430$). Sedentary collector/filterers were established as the dominant feeding category in enhancement gravel and remained so throughout the remaining sampling periods (42–66%).

DISCUSSION

As in other studies, macroinvertebrates colonized new substrate rather quickly after initial placement (Wise and Molles, 1979; Boulton *et al.*, 1988; Quinn *et al.*, 1998; McCabe and Gotelli, 2000; Zuellig *et al.*, 2002). Benthic macroinvertebrate densities and dry biomass was similar to that of undisturbed gravels within 6 weeks of gravel
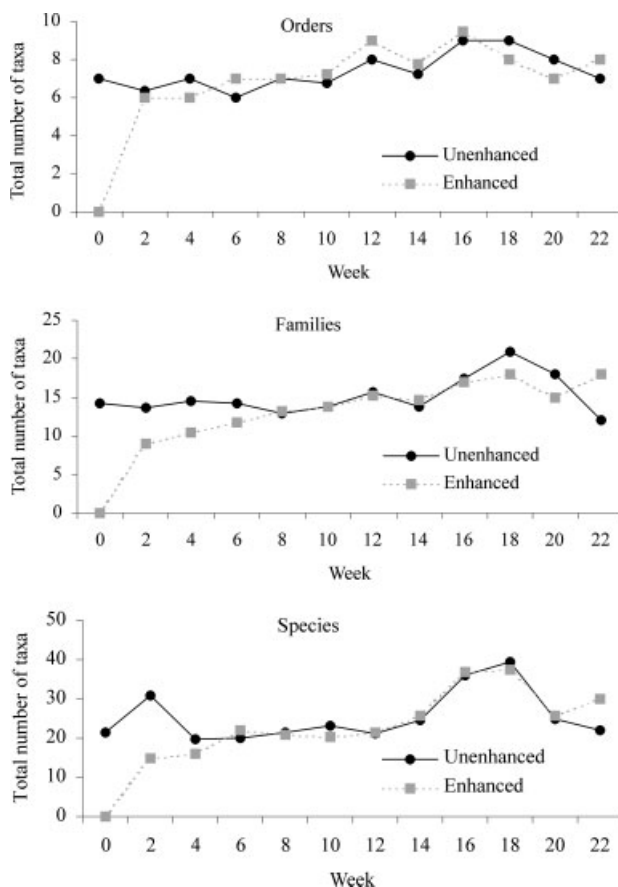
Figure 5. Total number of macroinvertebrate orders, families, and species per sampling period at seven Chinook salmon spawning gravel enhancement sites

placement and remained significantly higher in enhancement gravels to the end of the monitoring period (except Week 18; up to Week 22).

We speculate the higher densities and biomass observed were likely the result of four factors, in probable order of importance: (1) reduction of fines in enhancement gravel, (2) increase in habitat for collectors in enhancement gravels, (3) reduction of large predators, and (4) presence of nutrients in the new gravel. The increase in invertebrate production in stream enhancement sites has not been recorded in the literature, to our knowledge, although substrate particle size and permeability can have a significant effect on faunal distribution (Brusven and Prather, 1974; Marchant *et al.*, 1985; Beisel *et al.*, 1998). Overall surface bed material had fewer fines (<8 mm) after gravel placement and enhanced gravels were significantly more permeable than adjacent unenhanced bed material, suggesting possible benefits for invertebrate production (Merz and Setka, in press). Some studies discuss increasing aquatic system productivity through manipulation of nutrients, such as phosphorus (e.g. Perkins and Underwood, 2002). Sugunan (2000) suggests that increased productivity is observed in new reservoirs immediately after inundation due to phosphorus released from newly inundated soils. It is quite possible that increases in macroinvertebrate standing crop in new gravels may partially be explained by remnant soils from newly mined material providing some nutrient 'kick-start' for newly established organisms. Another important aspect is that the greatest number and biomass of benthic organisms within spawning habitat of the LMR is filter-feeding collectors. By increasing average water velocity within the sites, this feeding strategy may benefit by exploiting sites of increased food delivery (Smith-Cuffney and Wallace, 1987; Wetmore *et al.*, 1990). Shurin *et al.* (2002) compared indirect effects of predators on plants via herbivores (trophic cascades) in a wide variety of food webs. They found that in
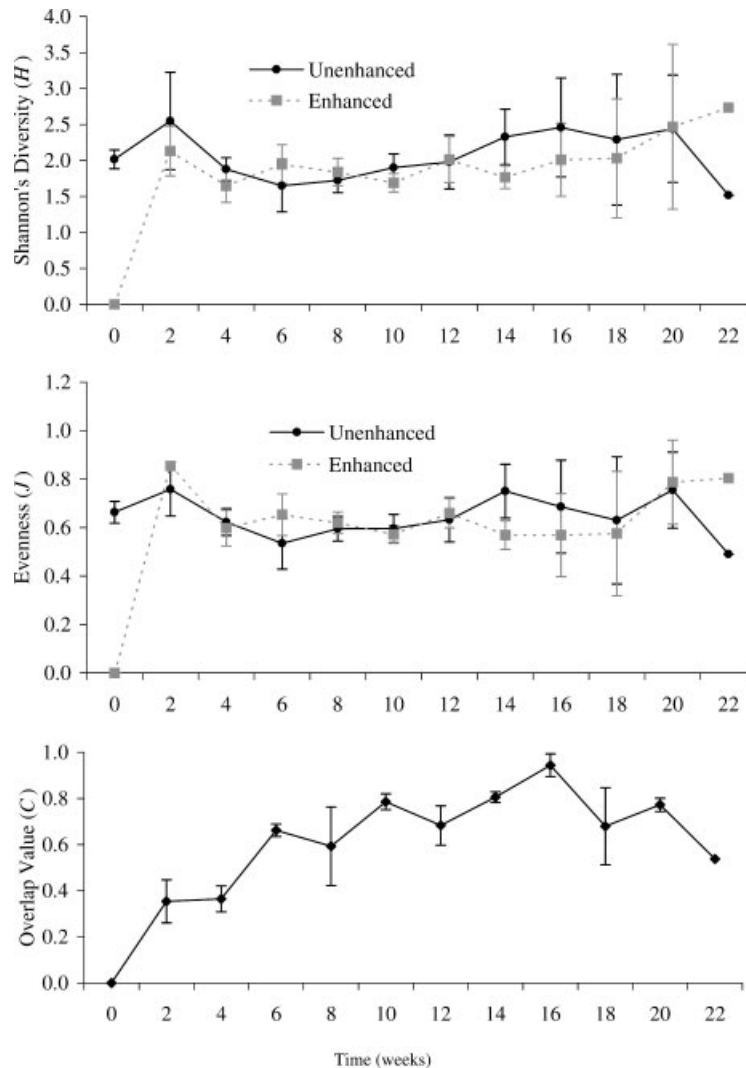
Figure 6. Mean (± 1 standard error) benthic macroinvertebrate diversity, evenness and species overlap for seven Chinook salmon spawning gravel enhancement sites

lotic studies, primary consumers had a positive response to predator removal. Although predatory macroinvertebrates were observed within the first sampling period of our study, prickly sculpin *Cottus asper*, the most common benthic predatory fish in LMR riffle habitat (Merz, 2002), were not collected in benthic samples until Week 6. Predatory fish can have a significant effect on local density of stream insects (Forrester, 1994). It is quite possible that all four mechanisms increased macroinvertebrate density and biomass within enhancement sites.

An interesting finding of this study is that macroinvertebrate density and biomass peaked in new gravels 6–12 weeks after placement (15 October to 30 November), roughly the same time length for Chinook salmon hatching and emergence (a 6–12 week period sometime between 15 December and 30 March) within the temperature regime of the lower Mokelumne River (Healey, 1991; Piper *et al.*, 1982). This suggests that appropriately timed gravel augmentation (approximately 1 November) may benefit juvenile salmonid production three-fold: by increasing spawning habitat, improving incubation parameters and increasing food availability for newly emerged fish.

We observed significantly lower species richness and diversity in the enhancement gravels only for the first sampling period after gravel placement. By Week 4, and subsequent sampling periods, we observed no significant
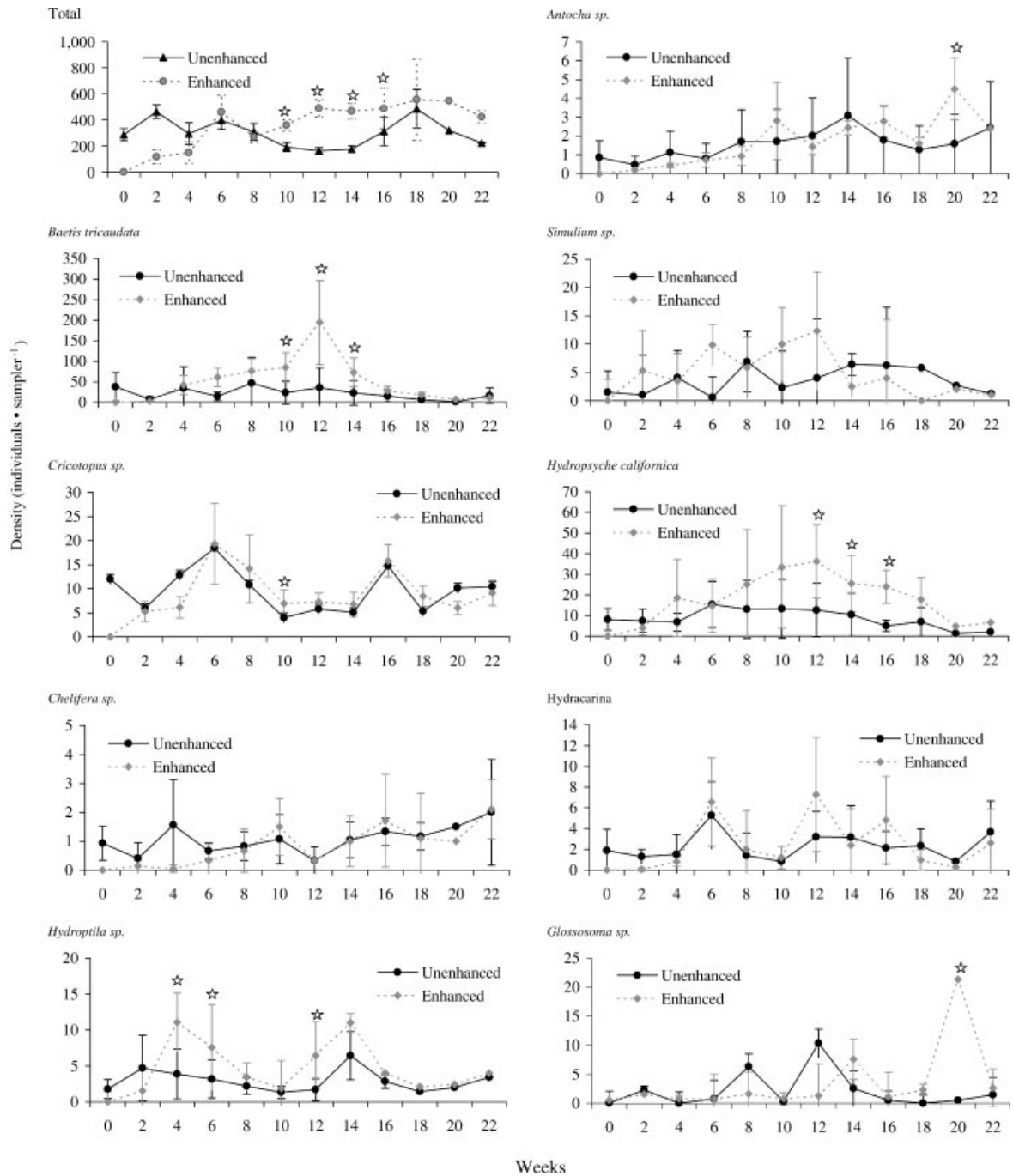
Figure 7. Total density and densities of macroinvertebrates (mean ± 95% Confidence Interval) in the nine most common species over time. Stars indicate significant differences

difference between enhanced and unenhanced gravel species richness or diversity. McCabe and Gotelli (2000) argue that because disturbance lowers abundance, fewer species per unit area in disturbed areas should be expected. However, even after macroinvertebrate densities equalled or surpassed those of unenhanced areas, we observed no significant change in the diversity or evenness of the benthic community. It is important to note, however, that species richness of the macroinvertebrate assemblage in the lower Mokelumne River is low. For example,

Unenhanced

Enhanced

Week

- ▨ Mobile collector/browser
- ▢ Piercers-herbivores
- ▨ Predator
- ■ Scrapers
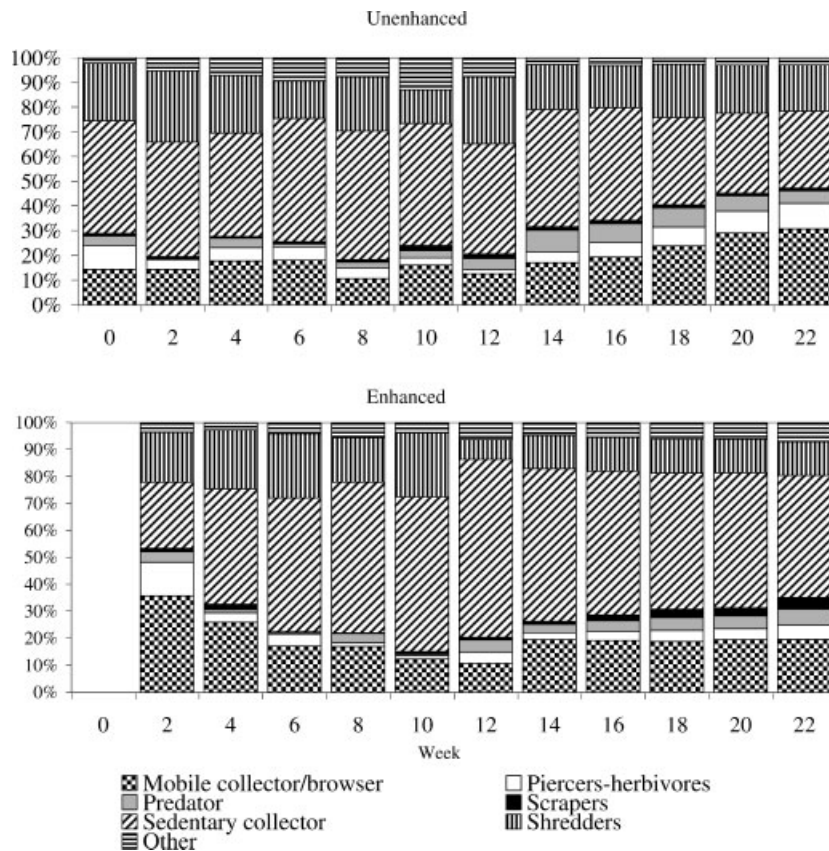- ▨ Sedentary collector
- ▥ Shredders
- ▤ Other

Figure 8. Mean relative abundance of functional feeding categories in unenhanced and enhanced gravels within Chinook salmon spawning habitat

although we have infrequently observed four plecopteran families in various monitoring efforts within the LMR, only five individual specimens (all Perlodidae) were observed during this monitoring project (<0.01% of total). Furthermore, one species of Tricoptera (*H. californica*) and two species of mayflies (*B. tricaudata* and *A. insignificans*) made up over 61% of total organisms sampled during this study. Influences of tailwater habitat, such as an altered sediment regime, changes to natural seasonality and variability of flow regimes (duration, extent and rate), and modified temperature range, may simply overshadow positive effects of small-scale gravel augmentation to invertebrate production, limiting potential improvements to the benthic macroinvertebrate community (Vannote and Sweeney, 1980; De Jalon *et al.*, 1994; Hawkins *et al.*, 1997). The lack of a source of diverse immigrants in areas upstream may also be an important limiting factor (MacArthur and Wilson, 1967; Simberloff and Wilson, 1969). Considering the impaired state of virtually all Central Valley streams at this elevation (Brown, 2000; Anon., 1995; Moyle, 1995), even if this habitat were improved to the point that it could support less tolerant species, source populations may simply not be available. Furthermore, even if they were available, 5 years may not be enough to allow for immigration and establishment of less tolerant organisms to enhanced sites (Muotka *et al.*, 2002).

We observed two distinct mechanisms for new gravel colonization over the 5-year study period. During 1996 and 1998, we observed flow fluctuations immediately after gravel placement (41–85% flow reduction). Mats of filamentous algae and aquatic plants (primarily *Egeria densa*, *Elodea canadensis* and *Rorippa nasturtium-aquaticum*) were observed floating into new gravel areas and taking root. Floating plants provided a seeding mechanism for *Daphnia pulex*, cyclopoid copepods, early instars of *B. tricaudata, A. insignificans, H. californica* and numerous small chironomids in the new gravel. Furthermore, we have observed an adult female Chinook

salmon dislodging aquatic vegetation upstream of an enhancement site during spawning activity and this material floated into the new gravel. During enhancement year 2000, no flow fluctuations were observed. Within 2 hours of gravel piling along the river's edge, larvae of *Glossosoma* sp. appeared on new gravel, and were observed crawling in from adjacent undisturbed material.

Our study demonstrates that cleaned gravels from adjacent floodplain materials can be quickly incorporated into the stream ecosystem. Benthic macroinvertebrate assemblages on salmonid spawning enhancement materials, as indicated by species richness, diversity and evenness, are similar to those of adjacent unenhanced spawning areas within 4 weeks of augmentation and can support higher benthic density and dry biomass for up to 22 weeks after placement. While increases in macroinvertebrate diversity were not apparent from such small-scale projects, colonization occurred rapidly and standing crop was increased indicating that such projects provide benefits beyond initial target species. Observation of scour and fill of new gravels in this and other studies (Merz and Setka, in press; Kondolf *et al.*, 1996) and the transient nature of alluvial systems suggest that these enhancement sites are transitory as are the site-specific benefits described here. Appropriate sediment budgets, flow regimes and reconnection of these processes with the flora and fauna of entire regulated streams must be incorporated into such enhancement work to realize long-term benefits.

REFERENCES

Allen MA, Hassler TJ. 1986. *Species Profiles: Life Histories and Environmental requirements of coastal fishes and invertebrates (Pacific Southwest) Chinook salmon*. United States Fish and Wildlife Service Biological Report 82 (11.49). United States Army Corps of Engineers, TR EL-82-4.

Andrews ED, Nankervis JM. 1995. Effective discharge and the design of channel maintenance flows for gravel-bed rivers. In *Natural and Anthropogenic Influences in Fluvial Geomorphology*, Costa JE, Miller AJ, Potter KW, Wilcock PR (eds). Geophysical Monograph 89. American Geophysical Union: Washington, DC; 151–164.

Anon. 1995. California Water Boards address impaired rivers. *Water Environment & Technology* **7**: 19–20.

Bauer SB, Burton TA. 1993. *Monitoring protocols to evaluate water quality effects of grazing management on Western rangeland streams*. Report 910/R-93-017. EPA: Washington, DC.

Beisel J, Usseglio-Polatera P, Thomas S, Moreteau J. 1998. Stream community structure in relation to spatial variation: the influence of meso-habitat characteristics. *Hydrobiologia* **389**: 73–88.

Bennett WA, Kimmerer WJ, Burau JR. 2002. Plasticity in vertical migration by native and exotic estuarine fishes in a dynamic low-salinity zone. *Limnology and Oceanography* **47**: 1496–1507.

Benoit HP, Post JR, Parkinson EA, Johnston NT. 1998. Colonization by lentic macroinvertebrates: evaluating colonization processes using artificial substrates and appraising applicability of the technique. *Canadian Journal of Fisheries and Aquatic Sciences* **55**: 2425–2435.

Boulton AJ, Spangaro GM, Lake PS. 1988. Macroinvertebrate distribution and recolonization on stones subjected to varying degrees of disturbance—an experimental approach. *Archiv für Hydrobiologie* **113**: 551–576.

Bowen SH. 1983. Quantitative description of diet. In *Fisheries Techniques*, Nielsen LA, Johnson DL (eds). American Fisheries Society: Bethesda, Maryland; 325–336.

Brasington J, Rumsby BT, Mcvey RA. 2000. Monitoring and modeling morphological change in a braided gravel-bed river using high resolution GPS-based survey. *Earth Surface Processes and Landforms* **25**: 973–990.

Brooks SS, Boulton AJ. 1991. Recolonization dynamics of benthic macroinvertebrates after artificial and natural disturbances in an Australian temporary stream. *Australian Journal of Marine and Freshwater Resources* **42**: 295–308.

Brown LR. 2000. Fish communities and their associations with environmental variables, lower San Joaquin River drainage, California. *Environmental Biology of Fishes* **57**: 251–269.

Brusven MA, Prather KV. 1974. Influence of stream sediments on distribution of macrobenthos. *Journal of the Entomological Society of British Columbia* **71**: 25–32.

CDC (California Department of Conservation). 1988. *Mineral land classification of Portland cement concrete aggregate in the Stockton-Lodi production-consumption Region*. Special Report 160. Division of Mines and Geology: Sacramento, California.

River Res. Applic. **21**: 61–74 (2005)

Collins BD, Dunne T. 1989. Gravel transport, gravel harvesting, and channel-bed degradation in rivers draining the southern Olympic Mountains, Washington, USA. *Environmental Geology and Water Sciences* **13**: 213–224.

De Jalon DG, Sanchez P, Camargo JA. 1994. Downstream effects of a new hydropower impoundment on macrophyte, macroinvertebrate and fish communities. *Regulated Rivers Reasearch and Management* **9**: 253–261.

Ebrahimnezhad M, Harper DM. 1997. The biological effectiveness of artificial riffles in river rehabilitation. *Aquatic Conservation: Marine and Freshwater Ecosystems* **7**: 187–197.

FERC (Federal Energy Regulatory Commission). 1998. *Order Approving Settlement Agreement and Amending License*. East Bay Municipal Utility District Lower Mokelumne River Hydroelectric Project No. 2916.

Forrester GE. 1994. Influences of predatory fish on the drift dispersal and local density of stream insects. *Ecology* **75**: 1208–1218.

Fuselier L, Edds D. 1995. An artificial riffle as restored habitat for the threatened Neosho madtom. *North American Journal of Fisheries Management* **15**: 449–503.

Gore JA. 1985. Mechanisms of colonization and habitat enhancement for benthic macroinvertebrates in restored river channels. In *The Restoration of Rivers and Streams: Theories and Experience*, Gore JA (ed.). Butterworth Publishers: Boston, Massachusetts; 81–102.

Gore JA, Crawford DJ, Addison DS. 1998. An analysis of artificial riffles and enhancement of benthic community diversity by physical habitat simulation (PHABSIM) and direct observation. *Regulated Rivers: Research and Management* **14**: 69–77.

Gørtz P. 1998. Effects of stream restoration on the macroinvertebrate community in the River Esrom, Denmark. *Aquatic Conservation: Marine and Freshwater Ecosystems* **8**: 115–130.

Groot C, Margolis L. 1991. *Pacific Salmon Life Histories*. University of British Columbia Press: Vancouver.

Hamilton IM, Barclay RM. 1998. Diets of juvenile, yearling, and adult big brown bats (*Eptesicus fuscus*) in southeastern Alberta. *Journal of Mammalogy* **79**: 764–771.

Hawkins CP, Hogue JN, Decker LM, Feminella JW. 1997. Channel morphology, water temperature, and assemblage structure of stream insects. *Journal of the North American Benthological Society* **16**: 728–749.

Healey MC. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). In *Pacific Salmon Life Histories*, Groot C, Margolis L (eds). University of British Columbia Press: Vancouver; 311–394

Hershey AE, Pastor J, Peterson BJ, Kling GW. 1993. Stable isotopes resolve the drift paradox for *Baetis* mayflies in an Arctic River. *Ecology (Tempe)* **74**: 2315–2325.

Hocking MD, Reimchen TE. 2002. Salmon-derived nitrogen in terrestrial invertebrates from coniferous forests of the Pacific Northwest. *BMC Ecology* **2**: 1–14.

Horn H. 1966. Measurement of 'overlap' in comparative ecological studies. *The American Naturalist* **100**: 419–424.

Kattelmann R. 1996. Hydrology and water resources. In *Sierra Nevada Ecosystem Project: Final Report to Congress, Volume II, Assessments and Scientific Basis for Management Options*, Centers for Water and Wildlife Resources (ed.). University of California: Davis; 855–920.

Kondolf GM. 1997. Hungry water: effects of dams and gravel mining on river channels. *Environmental Management* **21**: 533–551.

Kondolf GM, Mathews WVG. 1993. *Management of coarse sediment in regulated rivers of California*. Report Number 80. University of California Water Resources Center: Riverside.

Kondolf GM, Vick JC, Ramirez TM. 1996. Salmon spawning habitat rehabilitation on the Merced River, California: an evaluation of project planning and performance. *Transactions of the American Fisheries Society* **125**: 899–912.

Laasonen P, Muotka T, Kivijarvi I. 1998. Recovery of macroinvertebrate communities from stream habitat restoration. *Aquatic Conservation: Marine and Freshwater Ecosystems* **8**: 101–113.

Lake PS, Doeg TJ. 1985. Macroinvertebrate colonization of stones in two upland southern Australian streams. *Hydrobiologia* **126**: 199–211.

MacArthur RH, Wilson EO. 1967. *The Theory of Island Biogeography*. Princeton University Press: Princeton.

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

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

Maddock I. 1999. The importance of physical habitat assessment for evaluating river health. *Freshwater Biology* **41**: 373–391.

Mahoney JM, Rood SB. 1998. Streamflow requirements for cottonwood seedling recruitment: an integrative model. *Wetlands* **18**: 634–645.

Mangum F. 1986. Macroinvertebrates. In *Inventory and Monitoring of Wildlife Habitat*, Cooperrider AY, Boyd RJ, Stuart HR (eds). US Department of the Interior, Bureau of Land Management: Denver; 661–675.

Marchant R, Metzeling L, Graesser A, Sutter P. 1985. The organization of macroinvertebrate communities in the major tributaries of the LaTrobe River, Victoria, Australia. *Freshwater Biology* **15**: 315–331.

Menchen RS. 1961. *The Mokelumne River artificial spawning channel experiment 1960–61 spawning season*. Marine Resources Branch Administrative Report 61-3. California Department of Fish and Game.

Merritt RW, Cummins KW. 1996. *An Introduction to the Aquatic Insects of North America* (3rd edn). Kendall/Hunt: Dubuque.

Merz JE. 2002. Comparison of diets of prickly sculpin and juvenile fall-run Chinook salmon in the lower Mokelumne River, California. *The Southwestern Naturalist* **47**: 195–204.

Merz JE, Setka JD. 2004. Evaluation of spawning habitat enhancement for Chinook salmon in a regulated California River. *North American Journal of Fisheries Management* **24**: 397–407.

Moyle PB. 1995. Conservation of native freshwater fishes in the Mediterranean-type climate of California, USA: a review. *Biological Conservation* **72**: 271–279.

Muotka T, Paavola R, Haapala A, Novikmec M, Laasonon P. 2002. Long-term recovery of stream habitat structure and benthic invertebrate communities from in-stream restoration. *Biological Conservation* **105**: 243–253.

Nakamura T. 1999. Spawning activities of the fluvial Japanese charr *Salvelinus leucomaenis* and incubation of their eggs at the artificial spawning sites. *Nippon Suisan Gakkaishi, Tokyo* **65**: 434–440 (in Japanese with English abstract).

Negishi JN, Inoue M, Nunokawa M. 2002. Effects of channelisation on stream habitat in relation to a spate and flow refugia for macroinvertebrates in northern Japan. *Freshwater Biology* **47**: 1515–1529.

Palmer MA, Ambrose RF, Poff NL. 1997. Ecological theory and community restoration ecology. *Restoration Ecology* **5**: 291–300.

Pasternack GB, Wang CL, Merz JE. 2003. Application of a 2D hydrodynamic model to design of reach-scale spawning gravel replenishment on the Mokelumne River, California. *River Research and Applications* **19**: 1–21.

Pennak RW. 1989. *Fresh-water Invertebrates of the United States*. John Wiley and Sons: New York.

Perkins RG, Underwood GJC. 2002. Partial recovery of a eutrophic reservoir through managed phosphorus limitation and unmanaged macrophyte growth. *Hydrobiologia* **481**: 75–87.

Piper RG, McElwain IB, Orme LE, McCraren JP, Fowler LG, Leonard JR. 1982. *Fish Hatchery Management*. American Fisheries Society: Bethesda.

Platts WS, Megahan WF, Minshall GW. 1983. *Methods for evaluating stream, riparian, and biotic conditions*. General Technical Report INT-138. United States Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: Ogden, Utah.

Quinn GP, Lake PS, Schreiber ESG. 1998. A comparative study of colonization by benthos in a lake and its outflowing stream. *Freshwater Biology* **39**: 623–635.

Rosenberg DM, Resh VH. 1993. Introduction to freshwater biomonitoring and benthic macroinvertebrates. In *Freshwater Biomonitoring and Benthic Macroinvertebrates*, Rosenberg DM, Resh VH (eds). Chapman and Hall: New York; 1–9.

Rosenberg DM, Resh VH. 1996. Use of aquatic insects in biomonitoring. In *An Introduction to the Aquatic Insects of North America* (3rd edn), Merritt RW, Cummins KW (eds). Kendall/Hunt: Dubuque; 87–97.

Scruton DA, Clarke KD, Anderson TC, Hoddinott AS, Van Zyll De Jong MC, Houston KA. 1997. Evaluation of habitat improvement and restoration initiatives for salmonids in Newfoundland, Canada. *Canadian Manuscript Report of Fisheries and Aquatic Sciences* **2413**: 1–35.

Setka JD. 2001. *Fall-run Chinook salmon and steelhead trout spawning survey, September 2000 through March 2001 Mokelumne River, California*. East Bay Municipal Utility District: Orinda, California.

Shaw DW, Minshall GW. 1980. Colonization of an introduced substrate by stream macroinvertebrates. *Oikos* **34**: 259–271.

Shurin JB, Borer ET, Seabloom EW, Anderson K, Blanchette CA, Broitman B, Cooper SD, Halpren BS. 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters* **5**: 785–791.

Simberloff DS, Wilson EO. 1969. Experimental zoogeography of islands: the colonization of empty islands. *Ecology* **50**: 278–296.

Smith-Cuffney FL, Wallace JB. 1987. The influence of microhabitat on availability of drifting invertebrate prey to a net-spinning caddisfly. *Journal of the North American Benthological Society* **17**: 91–98.

Sommer TR, Nobriga ML, Harrell WC, Batham W, Kimmerer WJ. 2001. Floodplain rearing of juvenile Chinook salmon: evidence of enhanced growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 325–333.

Sugunan VV. 2000. Ecology and fishery management of reservoirs in India. *Hydrobiologia* **430**: 121–147.

Tikkanen P, Laasonen P, Muotka T, Huhta A, Kuusela K. 1994. Short-term recovery of benthos following disturbance from stream habitat rehabilitation. *Hydrobiologia* **273**: 121–130.

Townsend CR, Scarsbrook MR, Doledec S. 1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnology and Oceanography* **42**: 938–949.

Vannote RL, Sweeney BW. 1980. Geographic Analysis of Thermal Equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *American Naturalist* **115**: 667–695.

Waters TF. 1964. Recolonization of denuded stream bottom areas by drift. *Transactions of the American Fisheries Society* **93**: 311–315.

Wetmore SH, Mackay RJ, Newbury RW. 1990. Characterization of the hydraulic habitat of *Brachycentrus occidentalis*, a filter-feeding caddisfly. *Journal of the North American Benthological Society* **9**: 157–169.

Wheaton JM, Pasternack GB, Merz JE. 2004. Spawning habitat rehabilitation—1. Conceptual approach and methods. *International Journal of River Basin Management* **2**(1): 3–20.

Wiggins GB. 1998. *Larvae of the North American Caddisfly Genera (Trichoptera)* (2nd edn). University of Toronto Press: Toronto, Ontario.

Wise DH, Molles MC. 1979. Colonization of artificial substrates by stream insects: influence of substrate size and diversity. *Hydrobiologia* **65**: 69–74.

Zuellig RE, Kondratieff BC, Rhodes HA. 2002. Benthos recovery after an episodic sediment release into a Colorado Rocky Mountain River. *Western North American Naturalist* **62**: 59–72.