

## Aquatic Macrophyte Encroachment in Chinook Salmon Spawning Beds: Lessons Learned from Gravel Enhancement Monitoring in the Lower Mokelumne River, California

JOSEPH E. MERZ,\*<sup>1</sup> JAMES R. SMITH, MICHELLE L. WORKMAN, JOSE D. SETKA, AND BERT MULCHAEY

East Bay Municipal Utility District, 1 Winemasters Way, Suite K2, Lodi, California 95240, USA

**Abstract.**—We studied the effects of colonization of the spawning habitat of Chinook salmon *Oncorhynchus tshawytscha* by rooted aquatic macrophytes in a regulated central California river. At least seven species of plants invaded four spawning sites below the lowest nonpassable dam during an extended period of relatively low instream flows. The depths associated with aquatic vegetation were similar to those used by spawning salmon. Velocities were significantly lower where plants took root. As plants expanded over riffles, spawning females avoided those areas. We observed significant overall reductions in vegetation after flow events predicted to be of sufficient magnitude to mobilize substrates. However, the proportion of vegetation dislodged did not strongly correlate with the proportion of substrate that we predicted would mobilize. Even so, in areas where vegetation was reduced, use by salmon spawning subsequently increased. While shear stress may be part of the overall predictive equation for macrophyte control at spawning sites, other factors must be studied before a specific management action can be recommended.

Increased aquatic macrophyte abundance has been associated with river regulation throughout the world (see French and Chambers 1997). While macrophytes are important to primary production and contribute to habitat structure, substantial expansion in regulated North American and European streams can have negative consequences for salmonid species, including reduced dissolved oxygen within the water column, elevated hydrogen sulfide within the hyporheic zone and overall decreased spawning habitat value (Brooker et al. 1977; Bigelow 1996; Groves and Chandler 2005). Aquatic vegetation within the stream channel can influence bed shear stress, and shear stress in turn affects the growth and distribution of submergent vegetation (Nikora et al. 1998; Thompson et al. 2004). Managing vegetation with flow has the advantages of minimizing capital and annual costs and being environmentally neutral (Duan et al. 2006). While hydraulic engineers have traditionally viewed and analyzed aquatic vegetation as a roughness component that affects hydraulic efficiency, literature that examines the control of aquatic vegetation by manipulating the water resources system is limited (Duan et al. 2006).

In 2000, we observed several species of native and nonnative rooted aquatic macrophytes encroaching on

four spawning sites of Chinook salmon *Oncorhynchus tshawytscha* on the regulated lower Mokelumne River, California (LMR). These plants included common waterweed *Elodea canadensis*, leafy pondweed *Potamogeton foliosus*, smartweed *Polygonum* sp., Brazilian waterweed *Egeria densa*, water cress *Rorippa nasturtium-aquaticum*, water-starwort *Callitriche* sp., and water buttercup *Ranunculus aquatilis*. Our study was designed to determine whether the presence of aquatic macrophytes rooted in spawning gravels affected the selection of redd sites by spawning Chinook salmon, whether we could predict the instream flows necessary to dislodge vegetation from inundated spawning areas, and how spawning Chinook salmon have responded to rooted macrophyte manipulation in an engineered, enhanced spawning site.

The test hypotheses were as follows: (1) the depths and velocities associated with rooted macrophytes are similar to those associated with Chinook salmon redds; (2) the presence of aquatic macrophytes rooted in spawning gravels affects the selection of redd sites by spawning Chinook salmon; and (3) the areal extent of rooted vegetation is correlated with the estimated proportion of substrate mobilized at various flood flow releases.

### Study Site

The snow-fed Mokelumne River in California drains approximately 1,624 km<sup>2</sup> of the central Sierra Nevada (Figure 1). The river presently has 16 major water impoundments, including Camanche Reservoir (531,387,061 m<sup>3</sup>), which have altered the late spring

\* Corresponding author: jmerz@fishsciences.net

<sup>1</sup> Present address: Cramer Fish Sciences, 636 Hedburg Way, Number 22, Oakdale, California 95361, USA.

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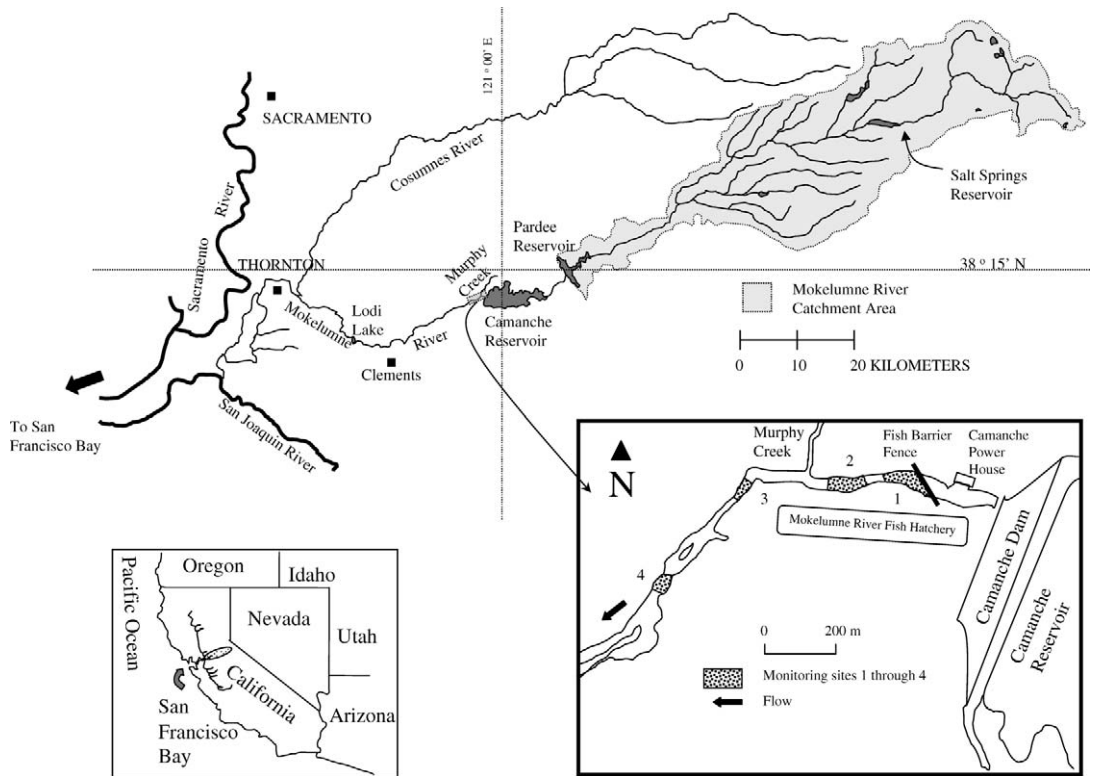


FIGURE 1.—Location of the study area within the Mokelumne River watershed.

snowmelt flow regime (see Pasternack et al. 2004; Wheaton et al. 2004). The LMR bed slope ranges from 0.10% near Camanche Dam (the lowest barrier to salmon) to 0.02% near the Cosumnes River confluence, the active channel now being half its former width (present average = 30 m; range = 19–43 m) and deepened. Camanche Dam blocks gravel delivery from upstream and historic mining operations depleted instream gravel storage, altering downstream riverbed complexity (Merz et al. 2006).

Presently, the LMR supports over 35 native (34%) and nonnative (66%) fish species, including native Chinook salmon (Workman 2003; Merz et al. 2004). Before completion of Camanche Dam in 1964, fall-run Chinook salmon spawned primarily between the town of Clements and about 4 km below Pardee Dam. A few fish spawned upstream of the canyon below Pardee Dam and downstream between Clements and Lockford (CDFG 1959). However, gravel and gold mining was widespread within the river during this period. The majority of salmon spawning now takes place in the 16-km reach between Camanche Dam at river kilometer (rkm; as measured from the confluence with the San Joaquin River) 102.2 and Clements (rkm 86.9;

Figure 1). Recent escapements to the Mokelumne River have ranged from 410 in 1991 to over 16,000 in 2005, although 36–87% return to the Mokelumne River Fish Hatchery (mean = 70%). River spawning generally occurs shortly after migration, primarily in late October through January. Fry emergence typically begins in late December and continues to the beginning of April.

Because spawning habitat is considered a limiting factor for Mokelumne River Chinook salmon reproduction (USFWS 1997), the river below Camanche Dam has been augmented with salmonid spawning gravel (typically 60–100 mm in diameter) since 1990; over 25,000 metric tons (14,000 m<sup>3</sup>) of material had been placed by 2006. The two primary goals of these enhancement projects are to improve existing habitat and increase total available spawning habitat. These projects typically consist of placing 382–1,147 m<sup>3</sup> of washed river rock (diameter = 25–150 mm) following predesigned configurations as a means of increasing the natural reproduction of Chinook salmon (See Pasternack et al. 2004). Sites are typically 30–100 m long and span the river channel. Gravel materials come from an adjacent open floodplain quarry (Merz and

Setka 2004). An estimated 55% of river Chinook salmon spawning now occurs in these enhancement sites (Mulchaey and Setka 2006). Between 2000 and 2001, rooted aquatic vegetation was observed encroaching on spawning gravels, including four enhancement sites immediately downstream of Camanche Dam (Figure 1, inset sites 1–4).

### Methods

For this study we summarized the information from several ongoing enhancement and monitoring projects. As a result, there is some variability in the data available for the four study sites.

*Spawning surveys and habitat measurements.*—Chinook salmon redd data have been collected since 1995 (Mulchaey and Setka 2006) following the methods described in Merz and Setka (2004). Briefly, Chinook salmon spawning surveys were conducted weekly within the study reach below Camanche Dam annually between September and January (Figure 1). Three surveyors canoed and walked downstream searching for signs of redd construction. Redd locations were recorded with a hand-held Global Positioning System (GPS) unit (Trimble Pathfinder Pro XR) and a laser range finder (Laser Atlanta Advantage). Location of each redd was downloaded from the GPS unit into an ESRI ArcView coverage. Depth and stream velocity were recorded on a random sampling of 5–10% of observed redds annually (118 within sites 1–4). Depth was recorded from a top-setting velocity rod, and depth-averaged velocity was approximated by assuming a logarithmic velocity profile and taking a measurement at 60% of the depth with an electromagnetic Flo-Mate flowmeter (Marsh McBirney, Inc.).

At sites 1 through 4, we collected data on water velocity and the presence or absence of aquatic plants every 0.5 m along four transects set perpendicular to the current (Figure 1). One transect was located roughly within the middle of each site. Depth and velocity were recorded as described above. We used a Student's *t*-test to compare channel depth and velocity at locations with and without rooted aquatic vegetation and to compare channel depths and velocities at locations with rooted aquatic vegetation and Chinook salmon redds.

The areal coverage of aquatic vegetation within site 1 (Figure 1) was recorded during October 2001. The leading edge of the aquatic vegetation was downloaded from a GPS unit into an ESRI ArcView coverage. Redd locations within site 1 before (1998, 1999, and 2000 spawning seasons) and after plant invasion (2001 and 2002 spawning seasons) were downloaded into an ESRI ArcView coverage. To compare the proportion of

redds built at sites before and after rooted vegetation invasion, we used a chi-square test.

*Substrate mobilization and effects of flood flow releases.*—Because aquatic vegetation is attached to the substrate with a shallow root system, we assumed that critical shear stress for surface grains within the spawning area would also dislodge aquatic vegetation (Friedman and Auble 1999). We estimated the critical shear stress for median particle size entrainment at four spawning sites (Figure 1) invaded by aquatic vegetation using the Shields (1936) equation as described in Smart (1999), that is,

$$\tau_c = f(\text{Re}) \cdot (\gamma_s - \gamma_f) d_i,$$

where  $\tau_c$  is the critical shear stress,  $f(\text{Re})$  is a function of the Reynolds number (from experimental data approximately 0.045 for  $\text{Re} > 1,000$ ),  $\gamma_s$  is the specific weight of sediment (assumed to be 25,990 N/m<sup>3</sup>),  $\gamma_f$  is the specific weight of water (9,807 N/m<sup>3</sup>), and  $d_i$  is the substrate particle size (m) of interest.

To determine substrate particle size, we collected surface substrate samples by pebble count at three randomly selected transects (~100 samples per transect) at sites 1–4 using methods similar to those of Bauer and Burton (1993). Three 30-m longitudinal transects were randomly placed at each site. Surveyors collected substrate samples by hand every 0.3 m along the transect and used a round-holed template to measure size. Substrate from pebble counts was categorized into 12 sizes: <8.0, 8.0, 16.0, 22.2, 31.8, 44.5, 63.5, 89.0, 127.0, 177.8, 254.0, and >254.0 mm. Categorization was based on the largest slot (round hole with specified diameter) through which an individual pebble could not be passed.

We then tested our prediction of rooted vegetation mobilization against three scheduled flood flow releases from Camanche Dam in the spring of 2003–2006 (Figure 2) to maintain a minimum flood storage capacity in Camanche Reservoir (USACE 1981). We incorporated the implementation of these releases in our sample design and sampled sites 1–4 by line intercept before and after the first flood flow release to determine the effect of increased releases on the presence of rooted aquatic vegetation in the spawning substrate. We established five transects, 10 m apart and perpendicular to the flow, at each of three sites (sites 1, 2, and 4) and two transects (10 m apart) at the smallest site (site 3). The presence or absence of rooted aquatic vegetation was determined by visual observation at 0.5-m intervals along each transect. Because of spawning gravel enhancement projects (see Merz et al. 2006) occurring within the LMR (encompassing sites 1 and 2), transects were repeated only at sites 3

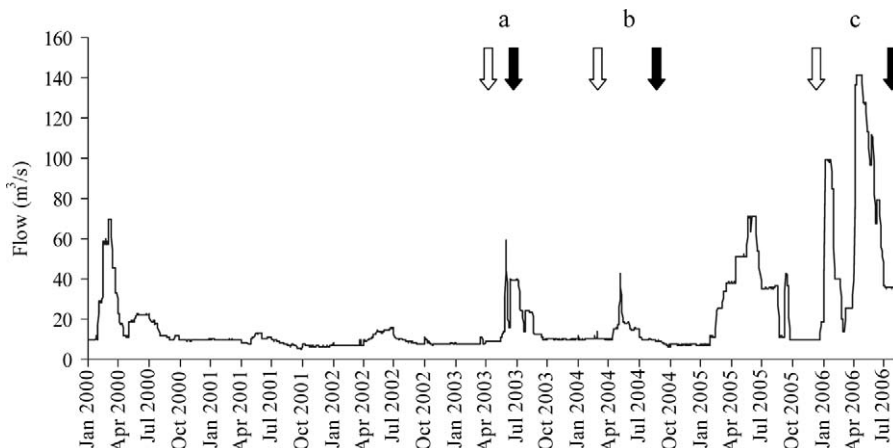


FIGURE 2.—Hydrograph of the lower Mokelumne River between 1 January 2000 and 1 August 2006. White arrows indicate preflow and black arrows postflow vegetation surveys. The sites surveyed during each period were as follows: (a) sites 1–4 (6 May–10 June 2003), (b) sites 3–4 (9 April–13 May 2004), and (c) sites 3–4 (8 December 2005–15 August 2006).

and 4 during two subsequent surveys in 2004 and 2006.

We used a chi-square 2 × 2 contingency test to assess changes in the proportion of vegetative cover before and after the modified flow releases. The substrate mobilization predicted from the estimated critical shear stress was then compared with the proportion of rooted aquatic vegetation mobilized at specific sites during test flows using the JMP linear regression model function, which performs an analysis of variance (ANOVA; Sall et al. 2001).

In 1999, 1,323 m<sup>3</sup> of spawning gravel was placed at site 2 (Figure 1). Over the following 4 years (2000–2003), we monitored salmon redds, conducted substrate pebble counts (see above), and determined presence or absence of rooted macrophytes. The monitoring encompassed the first flood release in 2003 but ended when vegetation was mechanically removed during a second placement of gravel in August 2004.

To assess the effects of vegetation coverage on spawning use at sites 1 and 2 before and after the flow manipulation, we used the JMP linear regression function, which performs an ANOVA (Sall et al. 2001).

**Results**

*Macrophyte Occurrence and Chinook Salmon Redds*

We determined the channel depth and velocity at 78 sample points along the four transects (45 with plants, 33 without plants; Table 1). There was no significant difference in channel depth at sites with and without rooted aquatic vegetation ( $t = 0.825$ ,  $df = 76$ ,  $P = 0.4122$ ). However, stream velocity was significantly

greater at sites without (mean = 0.55 m/s) than sites with rooted vegetation (mean = 0.46 m/s;  $t = 2.732$ ,  $df = 76$ ,  $P = 0.0078$ ).

Depth and velocity measurements were recorded at 53 Chinook salmon redds within sites 1 and 2 (Table 1). While the mean channel depth in areas with vegetation (62.6 cm) was significantly greater ( $t = -2.391$ ;  $df = 129$ ;  $P = 0.0182$ ) than mean channel depths of salmon redds (52.0 cm), the range of redd depths fell completely inside the depth range of aquatic vegetation at the site. The mean stream velocity associated with Chinook salmon redds (0.63 m/s) was significantly higher ( $t = 3.536$ ;  $df = 129$ ;  $P = 0.0006$ ) than that associated with vegetation (0.46 m/s). However, 85% of redds observed were found within the velocity range recorded with vegetation.

Chinook salmon constructed 593 redds in site 1 between September 1998 (1998 spawning season) and

TABLE 1.—Stream depth and velocity associated with aquatic macrophytes, uninvaded substrate, and Chinook salmon redds in the lower Mokelumne River.

Site characteristic		Depth (m)	Velocity (m/s)
Aquatic macrophytes absent	Average	0.63	0.55
	Minimum	0.06	0.02
	Maximum	1.16	1.09
	SD	0.31	0.23
Aquatic macrophytes present	Average	0.63	0.39
	Minimum	0.06	0.01
	Maximum	0.91	1.03
	SD	0.27	0.28
Chinook salmon present	Average	0.52	0.63
	Minimum	0.18	0.13
	Maximum	0.94	1.33
	SD	0.17	0.30

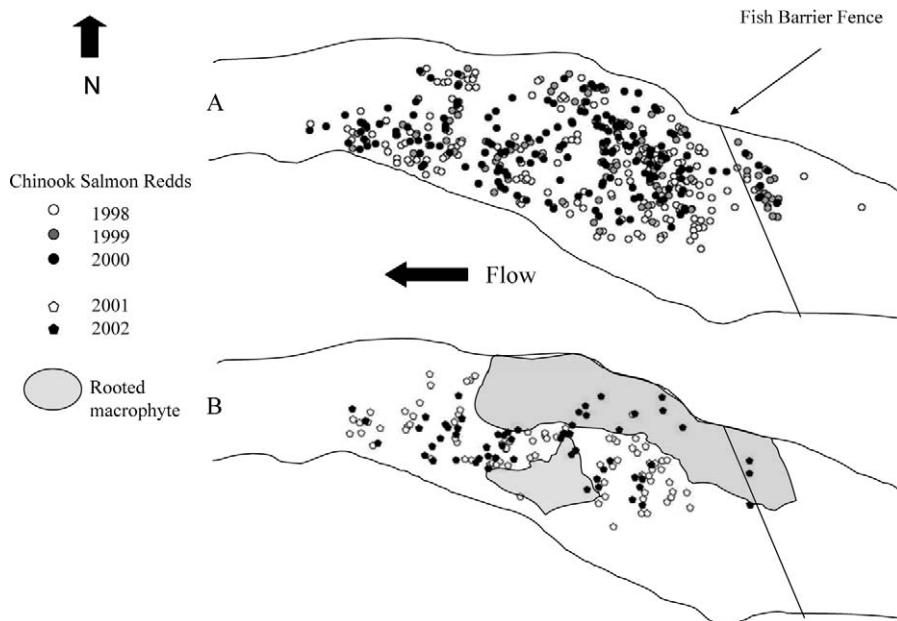


FIGURE 3.—Annual location of Chinook salmon redds within site 1 (A) before and (B) after vegetation expansion.

January 2003 (2002 spawning season; Figure 3). The average number of redds observed at site 1 annually before vegetation expansion was 109 (12% of total river redds). This dropped to 70.5 (8% of total river redds) for the 2 years after the expansion. A second augmentation of gravel at site 1 was performed in August 2003, ending the comparison. The presence of rooted aquatic vegetation significantly reduced the number of redds below what would be expected ( $\chi^2 = 32.464$ ;  $df = 592, 1$ ;  $P < 0.0001$ ).

#### *Estimates of Substrate Mobilization and Effects of Flood Flow*

Sediment mobilization estimates are provided in Tables 2 and 3. We estimated that the smallest ( $D_{10}$ ) substrate sizes (i.e., those with the median diameter at which 10% of the particles are smaller) within the four spawning sites would begin to mobilize at 2.2  $m^3/s$ . Flows in excess of 1,260  $m^3/s$  would be required to mobilize the largest substrate (178 mm) at all sites. Between 1 August 2000 and 29 May 2003, flows did not exceed 15.8  $m^3/s$  (mean = 5.1  $m^3/s$ ; Figure 2). We estimated that the peak flow during that period would mobilize only  $D_{10}$  at two of the four sites.

Peak flows of 42.7, 56.1, and 141.6  $m^3/s$  occurred on 5 May 2004, 30 May 2003, and 14 April 2006, respectively. During the initial survey in May 2004, sites had as much as 14.6–66.8% (mean = 38.6) coverage by aquatic vegetation. Estimates of substrate

mobilization explained less than 17% of the variation in actual vegetation removal during the study, and this was not statistically significant ( $F = 0.7832$ ;  $df = 1, 5$ ;  $P = 0.4262$ ). However, vegetation reduction was significantly higher at sites where we predicted movement (mean = 22% reduction) than sites where we predicted no change in vegetation cover (2% reduction;  $F = 18.5129$ ;  $df = 1, 5$ ;  $P = 0.0077$ ).

#### *Effect of Rooted Macrophyte Scour on Spawning Use in an Enhanced Spawning Site*

The areal coverage of site 2 by rooted aquatic plants gradually increased from less than 1% immediately after the fall 2000 gravel placement to over 66% in fall 2002. Spawning use at this site decreased from over 3% of available spawners using it in 2000 to 0.2% in 2002. Aquatic vegetation was reduced by 20% after a peak flow release of 56.1  $m^3/s$  in 2003 (Figure 4), and spawning use increased that same year to 1%. Areal coverage at site 2 explained over 99% of the variation in spawning use at the site. We found a significant relationship between the areal extent of rooted vegetation and the proportion of available spawners utilizing site 2 when vegetation was scoured by flow ( $F = 1,969.2$ ;  $df = 3, 1$ ;  $P = 0.0005$ ).

## Discussion

Macrophyte colonization of gravel streams can occur when velocities are low, and growth may be encour-

TABLE 2.—Calculations for theoretical entrainment of site-specific grain sizes at four spawning gravel enhancement sites on the lower Mokelumne River.

Variable or parameter <sup>a</sup>	Site-specific grain sizes <sup>b</sup>			1-phi grain sizes				
	D10	D50	D90	8 mm	16 mm	32 mm	64 mm	128 mm
<b>Constants</b>								
$\gamma_{\text{sediment}}$ (N/m <sup>3</sup> )	25,945	25,945	25,945	25,945	25,945	25,945	25,945	25,945
$\gamma_{\text{water}}$ (N/m <sup>3</sup> )	9,790	9,790	9,790	9,790	9,790	9,790	9,790	9,790
$f(\text{Re})$	0.045	0.045	0.045	0.045	0.045	0.045	0.045	0.045
$n$	0.043	0.043	0.043	0.043	0.043	0.043	0.043	0.043
<b>Site 1</b>								
$D_s$ (mm)	4.4	30.5	87.3	8	16	32	64	128
$D_s$ (m)	0.004	0.031	0.087	0.008	0.016	0.032	0.064	0.128
$\tau_c$ (N/m <sup>2</sup> )	3.20	22.17	63.48	5.82	11.6	23.3	46.5	93.0
$S$	0.0020	0.0020	0.0020	0.0020	0.0020	0.0020	0.0020	0.0020
$R$ (m)	0.163	1.132	3.242	0.297	0.594	1.188	2.376	4.752
$V_c$ (m/s)	0.31	1.13	2.28	0.46	0.73	1.17	1.85	2.94
$W$ (m)	44	44	44	44	44	44	44	44
$Q_c$ (m <sup>3</sup> /s)	2.2	56.3	325.0	6.05	19.21	61.0	193.6	615
<b>Site 2</b>								
$D_s$ (mm)	26.0	47.0	79.6	8	16	32	64	128
$D_s$ (m)	0.026	0.047	0.080	0.008	0.016	0.032	0.064	0.128
$\tau_c$ (N/m <sup>2</sup> )	18.88	34.17	57.89	5.82	11.6	23.3	46.5	93.0
$S$	0.0022	0.0022	0.0022	0.0022	0.0022	0.0022	0.0022	0.0022
$R$ (m)	0.876	1.586	2.688	0.270	0.540	1.080	2.160	4.320
$V_c$ (m/s)	1.00	1.48	2.11	0.46	0.72	1.15	1.82	2.89
$W$ (m)	30	30	30	30	30	30	30	30
$Q_c$ (m <sup>3</sup> /s)	26.2	70.4	169.4	3.68	11.68	37.1	117.7	374
<b>Site 3</b>								
$D_s$ (mm)	38.18	56.00	85.11	8	16	32	64	128
$D_s$ (m)	0.038	0.056	0.085	0.008	0.016	0.032	0.064	0.128
$\tau_c$ (N/m <sup>2</sup> )	27.75	40.71	61.87	5.82	11.6	23.3	46.5	93.0
$S$	0.0012	0.0012	0.0012	0.0012	0.0012	0.0012	0.0012	0.0012
$R$ (m)	2.362	3.465	5.266	0.495	0.990	1.980	3.960	7.920
$V_c$ (m/s)	1.43	1.84	2.44	0.50	0.80	1.27	2.02	3.20
$W$ (m)	29	29	29	29	29	29	29	29
$Q_c$ (m <sup>3</sup> /s)	96.9	183.4	368.6	7.16	22.74	72.2	229.2	728
<b>Site 4</b>								
$D_s$ (mm)	14.96	40.12	142.91	8	16	32	64	128
$D_s$ (m)	0.015	0.040	0.143	0.008	0.016	0.032	0.064	0.128
$\tau_c$ (N/m <sup>2</sup> )	10.87	29.16	103.89	5.82	11.6	23.3	46.5	93.0
$S$	0.0027	0.0027	0.0027	0.0027	0.0027	0.0027	0.0027	0.0027
$R$ (m)	0.411	1.103	3.930	0.220	0.440	0.880	1.760	3.520
$V_c$ (m/s)	0.67	1.29	3.01	0.44	0.70	1.11	1.76	2.80
$W$ (m)	31	31	31	31	31	31	31	31
$Q_c$ (m <sup>3</sup> /s)	8.4	43.4	360.7	2.95	9.38	29.8	94.6	300
<b>Overall</b>								
$D_s$ (mm)	22.25	49.92	98.75	8	16	32	64	128
$D_s$ (m)	0.022	0.050	0.099	0.008	0.016	0.032	0.064	0.128
$\tau_c$ (N/m <sup>2</sup> )	16.17	36.29	71.78	5.82	11.6	23.3	46.5	93.0
$S$	0.0029	0.0029	0.0029	0.0029	0.0029	0.0029	0.0029	0.0029
$R$ (m)	0.570	1.278	2.528	0.205	0.410	0.819	1.639	3.277
$V_c$ (m/s)	0.86	1.47	2.32	0.44	0.69	1.10	1.74	2.76
$W$ (m)	33	33	33	33	33	33	33	33
$Q_c$ (m <sup>3</sup> /s)	16.3	62.7	195.5	2.97	9.42	29.9	94.9	301
Mean $Q_c$								
Sites 1–4	33.4	88.4	305.9	5.0	15.8	50.0	158.8	504.0
Overall	12.4	37.8	125.4	2.0	6.3	20.0	63.4	201.3

<sup>a</sup> Re = the Reynolds number,  $n$  = the roughness coefficient,  $D_s$  = the specific substrate diameter,  $\tau_c$  = the critical shear stress for the entrainment of sediment,  $S$  = slope,  $R$  = hydraulic radius,  $V_c$  = critical velocity,  $W$  = the channel width, and  $Q_c$  = critical flow.

<sup>b</sup>  $D_{10}$  is the median diameter at which 10% of the particles are smaller and similarly for  $D_{50}$  and  $D_{90}$ .

TABLE 3.—Predicted mobilization of surface bed material and the observed reduction in the areal extent of rooted aquatic vegetation at four Chinook salmon spawning sites in the lower Mokelumne River.

Flow (m <sup>3</sup> /s)	Year	Site	Predicted mobilization (%)	Observed vegetation reduction (%)
56.1	2003	1	35.53	29.1
56.1	2003	2	39.3	20
56.1	2003	3	0	0.9
56.1	2003	4	46.8	0
56.1	2003	Average	42.05	12.5
42.7	2004	3	0	5.8
42.7	2004	4	37.3	0
141.7	2006	3	30	25.7
141.7	2006	4	74.5	11.3

aged by moderate velocities (Biggs 1996). Bigelow (1996) attributed “weed growth” and siltation of Chinook salmon spawning habitat on the upper Sacramento River, California, to an extended period of low flow releases from Keswick Dam. Similarly, the absence of flood flow releases in the LMR during the relatively dry August 2000 through May 2003 period

may have contributed to extensive growth of at least seven rooted aquatic plant species in the river channel associated with Chinook salmon spawning habitat. Common waterweed, leafy pondweed, smartweed, Brazilian waterweed, water cress, water-starwort, and water buttercup (which typically occur in slowly moving streams, rivers, and ponds [Hickman 1993]) created dense mats of vegetation in a portion of four Chinook salmon spawning sites of this regulated river. Aquatic macrophytes were able to colonize as much as 70% of individual Chinook salmon spawning sites immediately below Camanche Dam within 24 months of stable flows (mean = 9 m<sup>3</sup>/s), and this had a significant effect on spawning use.

According to Fritz et al. (2004b), the presence of the emergent macrophyte American water-willow *Justicia americana* appears to modify the stream environment by increasing the stability of streambed sediments and reducing current velocity, thereby enhancing deposition of fine sediments and organic matter. However, it is not always clear whether macrophytes biogenically

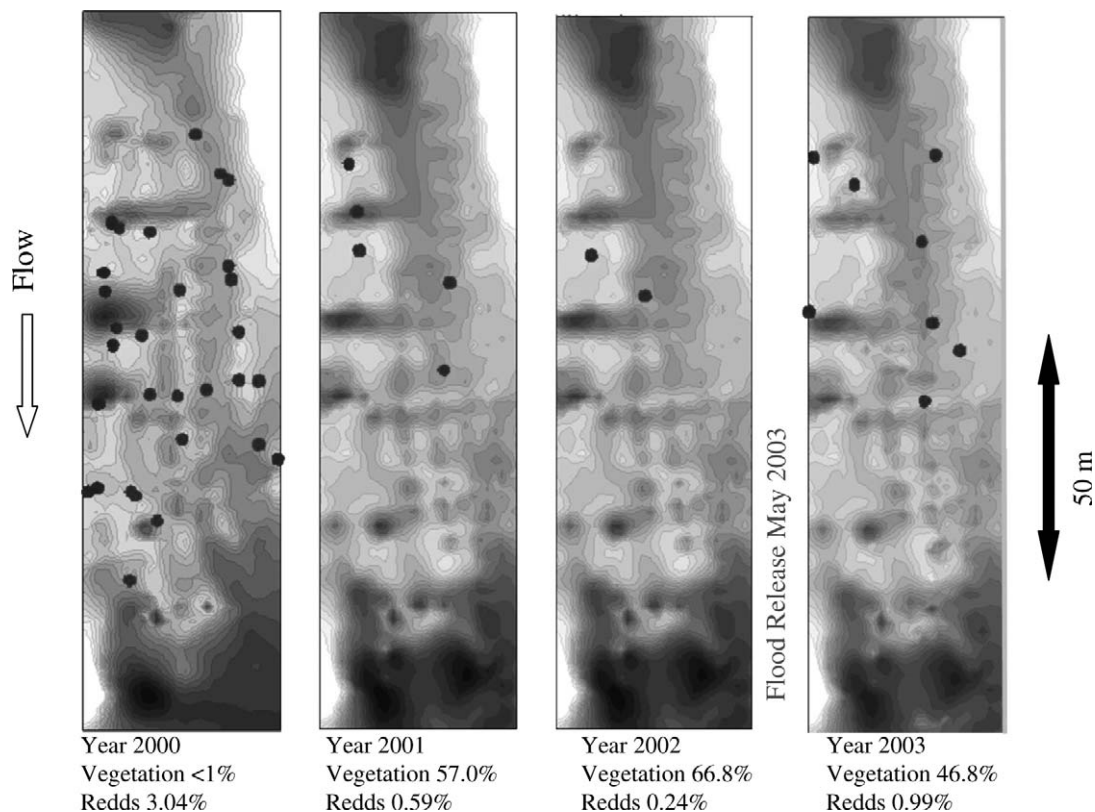


FIGURE 4.—Chinook salmon redds constructed at site 2 over four spawning seasons. The term “vegetation” refers to the percentage of the substrate covered by rooted vegetation, the term “redds” to the proportion of the redds in the Mokelumne River that were constructed at site 2.

enhance substratum stability or their presence merely reflects patches of stable substrate within the streambed (Fritz and Feminella 2003). Regardless of the mechanism, they found a clear association between beds of *J. americana* and streambed characteristics.

Our data show that the stream velocity at locations covered with rooted aquatic vegetation within Chinook salmon spawning sites was significantly lower than that at spawning areas devoid of vegetation. Additional drag exerted by plants reduces the mean flow velocity within vegetated regions, and plant form can have a significant effect on the mean flow field enhancing deposition of fine sediments and organic matter (Wilson et al. 2003; Fritz et al. 2004b). Although spawning substrate size selection was not directly measured in this study, salmonids tend to select coarse substrate that contains few fine particles (McNeil and Ahnell 1964; Hoopes 1972; Curry and Noakes 1995; Bernier-Bourgault and Magnan 2002), and this may partially explain their avoidance of vegetated areas. Furthermore, Pacific salmon do not feed while on spawning grounds, living off fat reserves. Energy conservation thus may play an important role in spawning success (Gilhousen 1980; Healey et al. 2004). While we did observe redds constructed within aquatic vegetation beds, numbers were greatly reduced from adjacent areas. The added energy required to dislodge aquatic vegetation from a potential redd within a relatively slower flow field may simply be cost prohibitive to most spawning females. This observation warrants additional study.

Flushing flows have been described as a programmed release of predetermined discharge for a given duration to remove fine sediments from river gravels (Reiser et al. 1989), and models have been prescribed for maximizing salmonid embryo survival using this method (Wu 2000). Flow manipulations (increasing stream velocity) correlate inversely with plant production (measured via biomass and chlorophyll; Biggs and Gerbeaux 1993; Biggs 1995). While there was no strong correlation between our estimated bed mobilization and the proportion of vegetation removed, we were able to estimate flows needed to mobilize substrates of varying size to dislodge invasive plants in Chinook salmon spawning beds below a large flood control dam, and this appears to have a positive effect on spawning use.

Fritz et al. (2004a) found that the biomass of *J. americana* was unrelated to disturbance by flooding as indicated by the likelihood of streambed movement by bank-full discharge. Similarly, our estimate of substrate mobilization for the various flow releases explained less than 17% of the variation in actual vegetation removal. Biggs (1996) emphasizes that the degree of

disturbance in a plant community for a given flow increase is dependent on both habitat resistance (armoring, imbrication, cohesiveness, and roughness) and biotic resistance from the plant (physical structure, which determines drag, anchoring strength, age of the community, and the shear stress to which it is acclimatized). Furthermore, under different conditions, rooted vegetation can have a variety of effects on channel sediment, including substrate armoring and increased lateral erosion (Clarke 2002). Therefore, a precise estimate of total vegetation removal was not achieved in this study.

Long-term hydraulic stability downstream of water storage reservoirs can contribute to increased aquatic macrophyte biomass over time. As we have shown, the magnitude of flow fluctuations is important in creating substrate mobility to dislodge macrophytes, but frequency may also play a role. Aquatic macrophytes may require tens of months to become well established in a streambed, and periods of stability longer than 1 year may encourage successful reinvasion (Biggs 1996). Mobilization of the largest substrate sizes measured would require flows over 1,000 m<sup>3</sup>/s above the release capacity of Camanche Dam (141.6 m<sup>3</sup>/s). Therefore, the magnitude and frequency of these hydraulic disturbances deserves further study (Jeffres et al. 2006). According to Ahearn et al. (2005), a temporal shift in NO<sub>3</sub>-N export within the regulated Mokelumne River may be contributing to accelerated plant growth in the reach immediately downstream of Camanche Dam and eventually to plant biomass loading to the downstream Sacramento–San Joaquin Delta. While we demonstrate flood release as a potential management tool for invasive macrophytes within the spawning reach immediately below a major flood control facility, it should be incorporated as a component of a flood control management strategy for regulated streams where problematic aquatic vegetation persists. The methods and results presented in this study should facilitate further development of such a tool and encourage future research.

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## References

- Ahearn, D. S., R. W. Sheibley, and R. A. Dahlgren. 2005. Effects of river regulation on water quality in the lower Mokelumne River, California. *River Research and Applications* 21:651–670.
- Bauer, S. B., and T. A. Burton. 1993. Monitoring protocols to evaluate water quality effects of grazing management on western rangeland streams. U.S. Environmental Protection Agency, Report EPA 910/R-93-017, Washington, D.C.
- Bernier-Bourgault, I., and P. Magnan. 2002. Factors affecting redd site selection, hatching, and emergence of brook trout, *Salvelinus fontinalis*, in an artificially enhanced site. *Environmental Biology of Fishes* 64:333–341.
- Bigelow, P. E. 1996. Evaluation of the Sacramento River spawning gravel restoration project and winter-run Chinook salmon redd survey data, 1987–1993. U.S. Fish and Wildlife Service, Red Bluff, California.
- Biggs, B. J. F. 1995. The contribution of disturbance, catchment geology, and land use to the habitat template of periphyton in stream ecosystems. *Freshwater Biology* 33:419–438.
- Biggs, B. J. F. 1996. Hydraulic habitat of plants in streams. *Regulated Rivers: Research and Management* 12:131–144.
- Biggs, B. J. F., and P. Gerbeaux. 1993. Periphyton development in relation to macroscale (geology) and microscale (velocity) limiters in two gravel-bed rivers, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 27:39–53.
- Brooker, M. P., D. L. Morris, and R. J. Hemsworth. 1977. Mass mortalities of adult salmon (*Salmo salar*) in the River Wye, 1976. *Journal of Applied Ecology* 14:409–417.
- CDFG (California Department of Fish and Game). 1959. The influences of proposed water projects on the fisheries of the lower Mokelumne River: Amador, Calaveras, and San Joaquin counties. CDFG, Sacramento.
- Clarke, S. J. 2002. Vegetation growth in rivers: influences upon sediment and nutrient dynamics. *Progress in Physical Geography* 26:159–172.
- Curry, R. A., and D. L. G. Noakes. 1995. Groundwater and the selection of spawning sites by brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 52:1733–1740.
- Duan, J. G., B. Barkdoll, and R. French. 2006. Lodging velocity for an emergent aquatic plant in open channels. *Journal of Hydraulic Engineering* 132:1015–1020.
- French, T. D., and P. A. Chambers. 1997. Reducing flows in the Nechako River (British Columbia, Canada): potential response of the macrophyte community. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2247–2254.
- Friedman, J. M., and G. T. Auble. 1999. Mortality of riparian box elder from sediment mobilization and extended inundation. *Regulated Rivers: Research and Management* 15:463–476.
- Fritz, K. M., M. A. Evans, and J. W. Feminella. 2004a. Factors affecting biomass allocation in the riverine macrophyte *Justicia americana*. *Aquatic Botany* 78:279–288.
- Fritz, K. M., and J. W. Feminella. 2003. Substratum stability associated with the riverine macrophyte *Justicia americana*. *Freshwater Biology* 48:1630–1639.
- Fritz, K. M., M. M. Gangloff, and J. W. Feminella. 2004b. Habitat modification by the stream macrophyte *Justicia americana* and its effects on biota. *Oecologia* 140:388–397.
- Gilhousen, P. 1980. Energy sources and expenditures in Fraser River sockeye salmon during their spawning migration. International Pacific Salmon Fisheries Commission, New Westminster, British Columbia.
- Groves, P. A., and J. A. Chandler. 2005. Habitat quality of historic Snake River fall Chinook salmon spawning locations and implications for incubation survival, part 2. Intragravel water quality. *River Research and Applications* 21:469–483.
- Healey, M. C., R. Lake, and S. G. Hinch. 2004. Energy expenditures during reproduction by sockeye salmon (*Oncorhynchus nerka*). *Behaviour* 140:161–182.
- Hickman, J. C., editor. 1993. The Jepson manual: higher plants of California. University of California Press, Berkeley.
- Hoopes, D. T. 1972. Selection of spawning sites by sockeye salmon in small streams. U.S. National Marine Fisheries Service Fishery Bulletin 70:447–458.
- Jeffres, C. A., A. P. Klimley, J. E. Merz, and J. J. Cech. 2006. Movement of Sacramento sucker, *Catostomus occidentalis*, and hitch, *Lavinia exilicauda*, during a spring release of water from Camanche Dam in the Mokelumne River, California. *Environmental Biology of Fishes* 75:365–373.
- McNeil, W. J., and W. H. Ahnell. 1964. Success of pink salmon spawning relative to size of spawning bed materials. U.S. Fish and Wildlife Service Special Scientific Report—Fisheries 469.
- Merz, J. E., G. B. Pasternack, and J. M. Wheaton. 2006. Sediment budget for salmonid spawning habitat rehabilitation in a regulated river. *Geomorphology* 76:207–228.
- Merz, J. E., and J. D. Setka. 2004. Evaluation of a spawning habitat enhancement site for Chinook salmon in a regulated California river. *North American Journal of Fisheries Management* 24:397–407.
- Merz, J. E., J. D. Setka, G. B. Pasternack, and J. M. Wheaton. 2004. Predicting benefits of spawning habitat rehabilitation to salmonid (*Oncorhynchus* spp.) fry production in a regulated California river. *Canadian Journal of Fisheries and Aquatic Sciences* 61:1433–1446.
- Mulchaey, B., and J. D. Setka. 2006. Fall-run Chinook salmon spawning survey, September 2005 through January 2006, Mokelumne River, California. East Bay Municipal Utility District, Orinda, California.
- Nikora, V. I., A. M. Suren, S. L. R. Brown, and B. J. F. Biggs. 1998. The effects of the moss *Fissidens rigidulus* (Fissidentaceae: Musci) on near-bed flow structure in an experimental cobble-bed flume. *Limnology and Oceanography* 43:1321–1331.
- Pasternack, G. B., C. L. Wang, and J. E. Merz. 2004. Application of a 2-D hydrodynamic model to design of reach-scale spawning gravel replenishment on the Mokelumne River, California. *River Research and Applications* 20:202–225.
- Reiser, D. W., M. P. Ramey, and T. A. Wesche. 1989. Flushing flows. Pages 91–135 in J. A. Gore and G. E.

- Petts, editors. Alternatives in regulated river management. CRC Press, Boca Raton, Florida.
- Sall, J., A. Lehman, and L. Creighton. 2001. JMP Start Statistics: a guide to statistics and data analysis. Duxbury, Pacific Grove, California.
- Shields, A. 1936. Application of similarity principles and turbulence research to bed load movement. Translated from the German by W. P. Ott and J. C. van Uchelen. U.S. Department of Agriculture, Soil Conservation Service Cooperative Laboratory, California Institute of Technology, Hydrodynamics Laboratory Publication 167, Pasadena, California.
- Smart, G. M. 1999. Turbulent velocity profiles and boundary shear in gravel bed rivers. *Journal of Hydraulic Engineering* 125:106–116.
- Thompson, C. E. L., C. L. Amos, and G. Umgiesser. 2004. A comparison between fluid shear stress reduction by halophytic plants in Venice Lagoon, Italy, and Rustico Bay, Canada: analyses of in situ measurements. *Journal of Marine Systems* 51:293–308.
- USACE (U.S. Army Corps of Engineers). 1981. Camanche Dam and Reservoir, Mokelumne River, California, water control manual. Appendix II to USACE, editor. Master manual of reservoir regulation of the San Joaquin River basin, California. USACE, Sacramento, California.
- USFWS (U.S. Fish and Wildlife Service). 1997. Revised draft restoration plan for the anadromous fish restoration program. USFWS, Washington, D.C.
- Wheaton, J. M., G. B. Pasternack, and J. E. Merz. 2004. Spawning habitat rehabilitation, II. Using hypothesis testing and development in design, Mokelumne River, California, USA. *International Journal of River Basin Management* 2:21–37.
- Wilson, C. A., T. Stoesser, P. D. Bates, and A. Batemann Pinzen. 2003. Open-channel flow through different forms of submerged flexible vegetation. *Journal of Hydraulic Engineering* 129:847–853.
- Workman, M. L. 2003. Lower Mokelumne River upstream fish migration monitoring conducted at Woodbridge Irrigation District Dam, August 2002 through July 2003. East Bay Municipal Utility District, Lodi, California.
- Wu, F. C. 2000. Modeling embryo survival affected by sediment deposition into salmonid spawning gravels: application to flushing flow prescriptions. *Water Resources Research* 36:1595–1603.