Predicting benefits of spawning-habitat rehabilitation to salmonid (*Oncorhynchus* spp.) fry production in a regulated California river

Joseph E. Merz, Jose D. Setka, Gregory B. Pasternack, and Joseph M. Wheaton

Abstract: We tested the hypothesis that spawning-bed enhancement increases survival and growth of chinook salmon (*Oncorhynchus tshawytscha*) embryos in a regulated California stream with a gravel deficit. We also examined how 12 physical parameters correlated within spawning sites and how well they predicted survival and growth of chinook salmon and steelhead (*Oncorhynchus mykiss*) embryos. Salmon embryos planted in enhanced gravels had higher rates of survival to the swim-up stage than embryos planted in unenhanced spawning gravels. No significant increase in growth was observed. Intergravel temperature and substrate size were strongly correlated with distance downstream from the lowest nonpassable dam. Intergravel turbidity and total suspended and volatile solids were also strongly correlated. Multiple-regression models were built with a combination of physical measurements to predict survival and length of salmon and steelhead embryos. Survival models accounted for 87% of the variation around the mean for salmon and 82% for steelhead. Growth models accounted for 95% of the variation around the mean for salmon and 89% for steelhead. These findings suggest that spawning-bed enhancement can improve embryo survival in degraded habitat. Additionally, measurements of a suite of physical parameters before and after spawning-bed manipulation can accurately predict benefits to target species.

Résumé : Nous avons éprouvé l'hypothèse selon laquelle l'aménagement des sites de reproduction augmente la survie et la croissance des embryons du saumon quinnat (*Oncorhynchus tshawytscha*) dans un cours d'eau de Californie soumis à la régulation et ayant une pénurie de gravières. Nous avons aussi déterminé la corrélation entre 12 variables physiques dans les sites de fraye et examiné comment elles peuvent prédire la survie et la croissance des embryons de saumons quinnat et de truites arc-en-ciel anadromes (*Oncorhynchus mykiss*). Les oeufs de saumons insérés dans des gravières améliorées ont une meilleure survie jusqu'au stade du début de la nage que ceux qui sont mis dans des gravières de fraye non améliorées. Il n'y a pas d'accélération significative de la croissance. La température dans le gravier et la taille du substrat sont en forte corrélation avec la distance en aval du barrage infranchissable le plus en aval. La turbidité dans le gravier, les solides totaux en suspension et les solides volatils affichent aussi la même forte corrélation. L'élaboration de modèles de régression multiple basés sur une combinaison de mesures physiques permettent de prédire la survie et la longueur des embryons de saumons quinnat et de truites arc-en-ciel anadromes. Les modèles de survie expliquent 87 % de la variation autour de la moyenne chez le saumon et 82 % chez la truite. Les modèles de croissance expliquent 95 % de la variation autour de la moyenne chez le saumon et 89 % chez la truite. Ces résultats montrent que l'amélioration des sites de fraye dans les habitats dégradés peut accroître la survie des embryons. De plus, la mesure des variables physiques avant et après la manipulation des sites de fraye peut permettre de prédire les avantages escomptés pour les espèces visées par l'aménagement.

[Traduit par la Rédaction]

Introduction

Salmonids have specific substrate and water-quality requirements for successful spawning, incubation, and embryo development. Riverine salmonids typically spawn in cool, clear, well-oxygenated streams with distinct depth, current velocity, and gravel size for each species (Bjornn and Reiser 1991; Groot and Margolis 1991). Salmonid eggs and embryos remain in the gravel for a relatively long time, ranging between roughly 2 and 8 months. The length of time between egg deposition and alevin emergence depends on species, redd location, and numerous physical parameters

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(DeVries 1997). Timing of spawning, egg burial depth, and embryo development are tied to the dynamic hydrologic regime of a river, including disturbances such as streambed scour (Montgomery et al. 1999).

Interannual mobilization of channel-bed sediment provides renewal of substrate conditions, and infrequent large floods reset spatially complex channel morphology (Trush et al. 2000). Alteration of flow, sediment transport, and continuity of river systems by dams, water diversions, levees, armoured banks, and mining may have deleterious affects on these processes, impacting upon one or more salmonid life stages (Nelson et al. 1987; Heaney et al. 2001; Soulsby et al. 2001). Elimination of a natural flow and sediment transport regime causes channel stabilization and narrowing, reduced formation of point gravel bars and secondary channels, accumulation of finer sediment in gravels, and reduced water quality (Poff et al. 1997). These physical degradations contribute to decreased substrate permeability and dissolved oxygen content (DO). Impaired water quality is presumed to cause a decrease in the health and survival of developing salmonid embryos within the substrate (Olsson and Persson 1988; Reiser and White 1988; Beacham and Murray 1990).

Since the early 1970s, numerous projects have been undertaken to ameliorate anthropogenic impacts on indigenous salmonid populations (House 1996; Scruton et al. 1997). In the Central Valley of California, 73 spawning habitat rehabilitation projects on 19 different rivers were carried out between 1976 and 1999, but their success has been poorly evaluated (Kondolf et al. 1996; Wheaton 2003). Nevertheless, concerns over the fate of California Central Valley steelhead (*Oncorhynchus mykiss*) and several runs of chinook salmon (*Oncorhynchus tshawytscha*) resulted in the United States National Marine Fisheries Service (NOAA) listing these populations as threatened or endangered under the Endangered Species Act (NOAA 1994, 1998). Salmonid spawning-habitat rehabilitation within California has received increasing attention as a tool to enhance these dwindling populations (Buer et al. 1981; Kondolf and Mathews 1993; California Department of Water Resources 2002). Wheaton (2003) developed a systematic approach to designing salmon spawning habitat rehabilitation projects using spawning-bed enhancement. While gravel augmentation typically entails dumping of appropriate materials in or near the channel to allow distribution via stream flow, spawning-bed enhancement involves placement of gravel as specific bed features (typically riffles or bars), potentially providing immediate spawning habitat. Merz and Setka (2004) showed that spawning-bed enhancement not only attracted spawning salmon to previously unused areas, but improved intergravel physical parameters associated with spawning and embryo development. Spawning-bed enhancement has been shown to benefit nontarget aquatic fauna as well (Merz and Chan 2004). Yet there is much uncertainty as to how well projects mitigate degradation of spawning habitat or improve survival of developing embryos (Roni et al. 2002). Additional research is needed to evaluate how substrate and associated hyporheic environment directly influence embryo survival (Kondolf et al. 1996; Merz and Setka 2004). In this paper, results from two embryo-survival experiments are reported. In the first experiment, we test the hypothesis that spawning-bed enhancement increases survival and growth of riverine chinook salmon embryos to the swim-up stage. In the second experiment, we propose embryo survival and growth models based on measurable physical parameters. We then test the validity of four multiple-regression models to predict the benefits of spawning-habitat enhancement on developing chinook salmon and steelhead embryos in a regulated California river.

Material and methods

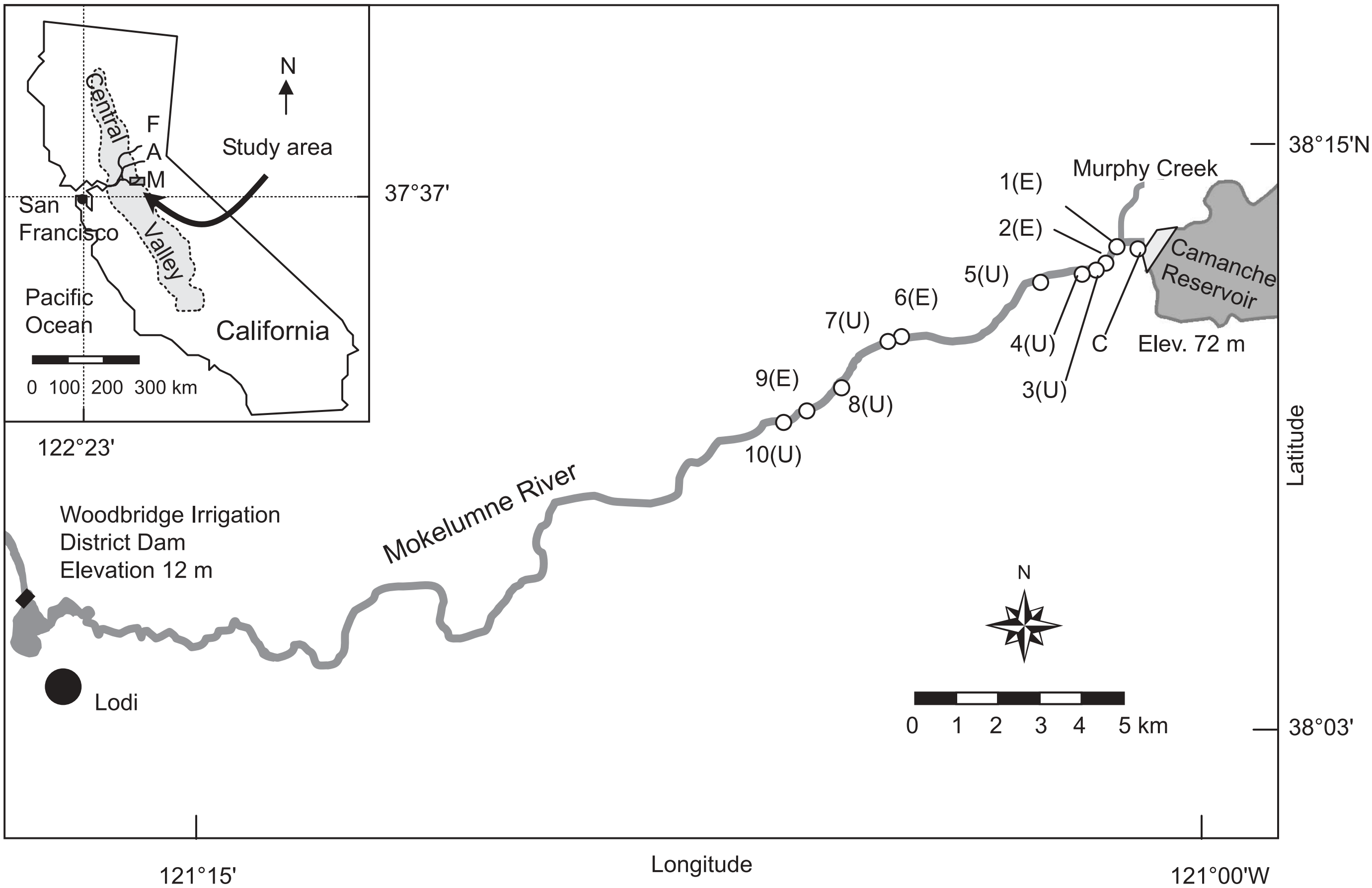
Study site

The Mokelumne River, California, drains approximately 1624 km^2 of the central Sierra Nevada. Sixteen major dams or diversions, including the 0.24-km^3 Pardee and the 0.51-km^3 Camanche reservoirs, have dramatically altered the flow regime of the lower Mokelumne River (LMR) (Pasternack et al. 2004). Prior to completion of the Camanche Dam in 1964, annual peaks exceeded 200 m$^3 \cdot s^{-1}$ for 21 of 57 years. Since 1964, annual peaks have never exceeded 200 m$^3 \cdot s^{-1}$, with the discharges associated with the 2-, 5-, 10-, and 100-year recurrence intervals decreased by 67%, 59%, 73%, and 75%, respectively.

The LMR is approximately 54 km of regulated river between Camanche Dam, a nonpassable barrier to anadromous fish, and its confluence with the Sacramento – San Joaquin Delta. The river between Camanche Dam and Lake Lodi (Fig. 1), is characterized by alternating bar-complex and flatwater habitats, and is above tidal influence, with a gradient of approximately 0.00017. The drainage consists of 87 km^2 of mostly agricultural and urbanized land. Several small streams and storm drains enter the lower river. At least 35 fish species occur in the LMR, including two native anadromous salmonids, fall-run chinook salmon, and winter steelhead (Merz 2001). Both populations are supplemented by Mokelumne River Fish Hatchery (MRFH) production and fish imported from the Feather River and Nimbus (American River) hatcheries. Most chinook salmon and steelhead spawning on the LMR now takes place in the 14-km reach immediately below Camanche Dam.

Compared with other major barriers on Sierra rivers, Camanche Dam is positioned in an area of relatively low elevation and relief. Accordingly, slopes throughout the current spawning reaches remain low (ranging from 0.0005 to 0.0020). Tailings from abandoned gravel-mining operations are frequent along the upper 11 km of the LMR. While many of the tailings are isolated from the river by berms and levees, several large pits are now incorporated into the main river channel. It has been estimated that approximately 80% of historical spawning habitat is now inaccessible, owing to construction of Camanche Dam, and remaining habitat quality is a limiting factor to Mokelumne River salmonid production, second only to ocean harvest (Menchen 1961; Federal Energy Regulatory Commission 1993). East Bay Municipal Utility District, owner and operator of Camanche Dam, has placed over 11 000 m^3 of gravel at 12 spawning-bed enhancement sites along the LMR since 1991 and has a monitoring program encompassing all of these projects that will extend to at least 2009 (Pasternack et al. 2004). The projects typically consist of placing approximately 350–1200 m^3 of washed river rock in berms, staggered bar, riffle, or complex channel geometry configurations to improve

Fig. 1. Locations of 10 egg-tube study sites (○) within the lower Mokelumne River, California. C, Mokelumne River Hatchery (control); E, enhanced site; U, unenhanced site; F, Feather River; A, American River; M, Lower Mokelumne River.



spawning habitat. Chinook salmon and steelhead typically begin spawning in the new gravels within 3–24 months of gravel placement. For this study, 10 sites were evaluated based on access and how many could be assessed within a single day. The sites are spread out within the upper 11.3 km of the LMR, four of them being spawning bed enhancement sites (Fig. 1).

Egg-incubation tubes

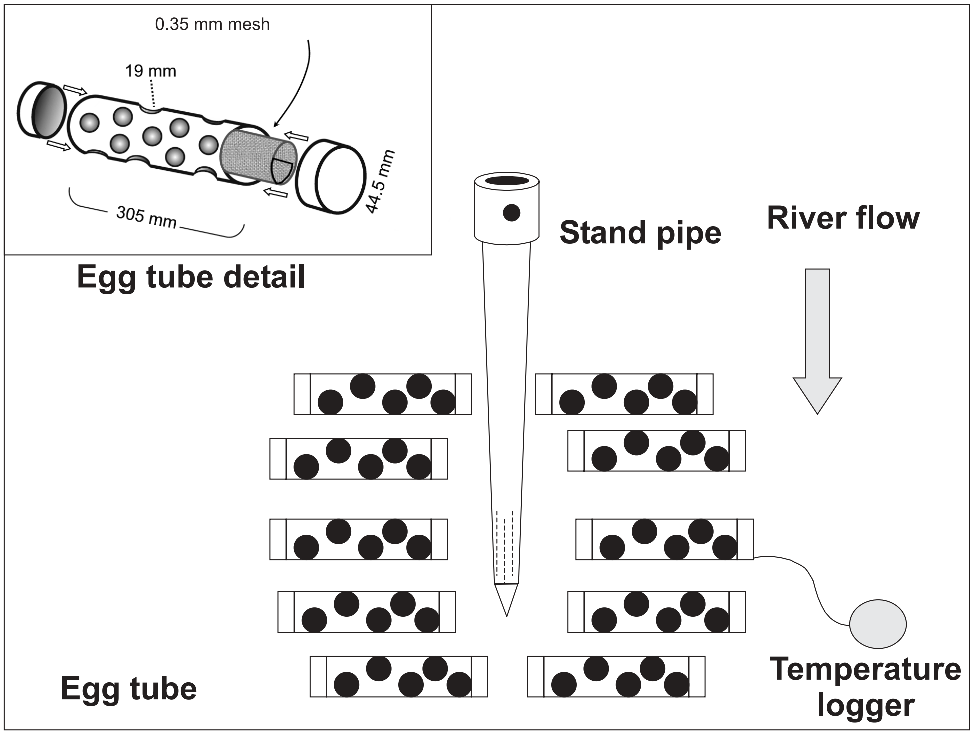
The focus of the first experiment was to compare survival and growth (as indicated by length) of chinook salmon embryos in enhanced and unenhanced spawning gravel sites. The second experiment was conducted to develop a predictive model of chinook salmon and steelhead survival and growth using associated physical parameters within spawning beds. In both experiments, egg-incubation tubes were buried in gravels to test survival and growth of fertilized eggs and embryos.

Egg tubes were constructed of standard dimension ratio 35-polyvinyl chloride (PVC) pipe with two PVC caps to close the tube ends (Fig. 2). Eighteen, evenly spaced, 19-mm-diameter holes were drilled into each tube. The tube's inner surface was covered with 0.35 mm mesh plastic screen typically used for egg incubation in steelhead and chinook salmon hatcheries (Leitritz and Lewis 1980). An artificial "redd" was constructed at each site for egg-tube placement. A series of depressions were made by hand in the gravel streambed for each set of egg tubes (Fig. 2). Pockets were constructed in an upstream progression, following the description of DeVries (1997). At each study site, egg-incubation tubes were buried horizontally and perpendicular to stream flow at a depth of 22 cm, the approximate depth of egg pockets in chinook salmon and steelhead redds according to Healey (1991) and Montgomery et al. (1999). Bed material from subsequent pockets was used to cover each egg tube.

Experiment 1: survival and growth in enhanced versus unenhanced sites

To compare survival of chinook salmon embryos in enhanced and unenhanced gravel sites, egg tubes were buried at four enhanced-substrate locations (constructed between 1994 and 2001) and six unenhanced-substrate locations within the LMR (Fig. 1). Unenhanced sites were selected on the basis of consistent spawning use by chinook salmon and accessibility. Ten tubes with approximately 200 chinook salmon eggs each from the MRFH were buried at each site. A control group of 2000 eggs was placed in incubation tubes (200 eggs each) at the MRFH to monitor embryo development. Eggs were taken from approximately 22 female chinook salmon at the MRFH on 21 November 2001. Fertilized eggs were "eyed" and 18 days old (average hatchery water

Fig. 2. Diagram of constructed "redd" with egg tubes, stand pipe, and temperature logger (top view). The figure is not drawn to scale.



temperature was 12.3 °C) when placed in the egg tubes and buried in the gravel. MRFH water is sand-filtered and piped from Camanche Reservoir.

Experiment two: predictive models of survival and growth

To test predictive models of chinook salmon and steelhead embryo survival and growth from associated physical measurements, approximately 20 000 chinook salmon and steelhead embryos were buried in egg tubes at various spawning habitats located throughout the LMR (see Habitat selection and evaluation below). Five tubes with approximately 200 eyed chinook salmon embryos and five tubes with approximately 200 eyed steelhead embryos were buried at each site. A control group of five chinook salmon egg tubes and five steelhead egg tubes (200 embryos each) were placed in rearing troughs at the MRFH to monitor embryo development and survival. Chinook salmon eggs were taken from 15 female salmon spawned on 23 December 2001 at the MRFH. Fertilized eggs were eyed and 18 days old (average hatchery water temperature was 10.12 °C) when placed in egg tubes and buried in the gravel on 9 January 2002. An insufficient number of steelhead spawned at the MRFH to provide embryos for this study, therefore eggs were taken from 12 female steelhead spawned on 18 December 2001 at the Feather River Hatchery, California. Fertilized steelhead eggs were approximately 22 days old when placed in the egg tubes and buried in the gravel on 9 January 2002 (average hatchery water temperature was 10.3 °C).

Habitat selection and evaluation

For experiment 2, 10 sites were selected within the upper 11.3 km of the LMR, based on historical spawning use and enhancement activities (Fig. 1). Although, the sites were located in the vicinity of experiment 1 sites, the sites did not overlap and were not selected on the basis of enhanced versus unenhanced gravels. The 10 sites each consisted of similar riffle morphologies with comparable substrate compositions ($D_{50} \approx$ 150–450 mm gravels), channel slopes (0.002–0.006) and hydraulic conditions (shallow (<0.36 m), and swift current (>0.6 $m \cdot s^{-1}$). Hydraulics at each site were crudely characterized from one point measurement of depth and velocity positioned between the egg tube placement locations (at the standpipe location; Fig. 2). This measurement was performed on 9 December 2001 during a discharge of 6.5 $m^3 \cdot s^{-1}$, which was representative of hydraulics experienced throughout the incubation period. 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 Marsh McBirney Flo-Mate velocimeter.

Substrate evaluation

Both surface and subsurface grain-size distributions were used to characterize the substrate during the post-study period (after egg-tube removal) at each site. Grain-size distributions were assumed not to have changed from pre- to post-analysis based on previous studies (Merz and Setka 2004). Subsurface samples were collected at the location of the standpipe at each site using a McNiel core sampler (St-Hilaire et al. 1997). Samples were placed in sealed containers and transported to the laboratory for analysis. Substrate was sieved through screens of the following sizes: 0.5, 1.0, 2.4, 4.7, 9.5, 12.7, 15.9, 22.2, 31.8, 44.5, 63.5, 88.9, 127.0, 177.8, and 254.0 mm. Each size class was weighed and recorded. Residual water and associated suspended sediment was poured through 15-cm No. 595 filter paper. The paper and sediment residual was dried at 70 °C for 24 h, weighed,

Table 1. Observed survival rates and total lengths (TL) of chinook salmon embryos incubated in egg tubes from 12 December 2001 through 7 January 2002 and from 9 January through 31 January 2002 at the Mokelumne River Fish Hatchery and at four enhanced and five unenhanced spawning sites.

Experiment/group	Species	Mean survival rate (%)	SE*	Lower 95%	Upper 95%	Mean TL (mm)	SE*	Lower 95%	Upper 95%
Experiment 1									
Hatchery	Chinook salmon	60	0.05	0.50	0.70	26.9	0.38	26.19	27.68
River									
Enhanced sites	Chinook salmon	29	0.03	0.24	0.35	25.2	0.12	24.77	25.55
Unenhanced sites	Chinook salmon	22	0.02	0.18	0.26	25.1	0.02	24.81	25.43
Experiment 2									
Hatchery	Chinook salmon	88	0.04	0.76	1.00	22.6	0.44	21.32	23.78
	Steelhead	84	0.08	0.62	1.00	22.2	0.19	21.69	22.73
River gravel	Chinook salmon	58	0.04	0.50	0.65	18.5	0.84	16.81	20.21
	Steelhead	61	0.03	0.54	0.68	19.0	0.89	17.20	20.79

*A pooled estimate of error variance was used.

and recorded. Surface samples were collected by pebble count at three randomly selected transects (~100 samples per transect) at each site 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.

Intergravel permeability, DO, temperature, and turbidity

Intergravel water-quality measurements were taken at each site prior to egg-tube placement and immediately after egg-tube removal. A modified Terhune Mark VI standpipe was driven into the gravel to measure gravel permeability, DO, and water temperature following Barnard and McBain (1994). We collected water samples from the standpipe with a vacuum hand pump apparatus (Saiki and Martin 1996). Samples were taken at depths of 15, 30, and 45 cm to evaluate stratification of compaction and sedimentation within the known depth ranges of chinook salmon and steelhead spawning (Vronskiy 1972; Chapman 1988; Bjornn and Reiser 1991). Approximately 200 mL of water was collected from each sample and transported to the laboratory to measure turbidity in nephelometric turbidity units (NTU), total suspended solids (TSS), and volatile suspended solids (VSS). Turbidity was measured with a Hach 2100P turbidimeter. TSS samples were filtered through a 50-µm sieve, then passed through a precombusted gas fiber filter, dried to 60 °C, and weighed (American Public Health Association et al. 1995). Ambient DO and stream temperature (15 cm below the water surface) as well as intergravel DO and water temperature were recorded with a YSI 55 dissolved-oxygen meter. An Onset StowAway TidbiT temperature logger (–4 °C to +37 °C) was buried with the eighth tube (starting with top left tube No. 1) at each monitoring location (Fig. 2). Loggers recorded water temperature within the gravel every 60 min for the duration of the monitoring period (approximately 26 days). Hourly temperature data were totaled to calculate temperature-hours for each site.

Survival, development, and general condition

Based on observation of the hatchery control group, egg tubes were removed from the gravel when embryos reached the alevin stage and at least 10% showed capability of self-orientation in water current, typical of the swim-up stage. Live alevins were counted, measured for total length (TL), and assessed for anomalies (such as disease or deformities). Alevin mortalities and unhatched embryos were enumerated and recorded.

Data analyses

We used a one-way *t* test to compare mean survival rates and lengths of chinook salmon alevins buried in enhanced and unenhanced gravels (Zar 1999). To build a survival and growth model for chinook salmon and steelhead embryos, principal components analysis (PCA) was used to reduce the number of physical condition variables in the data set. This analysis was performed with SPSS® version 10 (SPSS Inc. 1997). We used the B4 selection method, as described in Joliffe (1972) and prescribed by Talmage et al. (2002), to select representative environmental variables indicated by the first four axes. We used multiple linear regression to build preliminary models with these independent variables to predict mean survival and mean TL of chinook salmon and steelhead alevins using the JMP linear regression model function, which performs an analysis of variance (ANOVA) (Sall et al. 2001). Alternate variables were then exchanged to strengthen the models. We also used ANOVA to compare the independent variables with alevin survival and TL. A significance level of 0.05 was used in statistical tests.

Results

Experiment 1: chinook salmon embryo survival and growth in enhanced and unenhanced spawning gravels

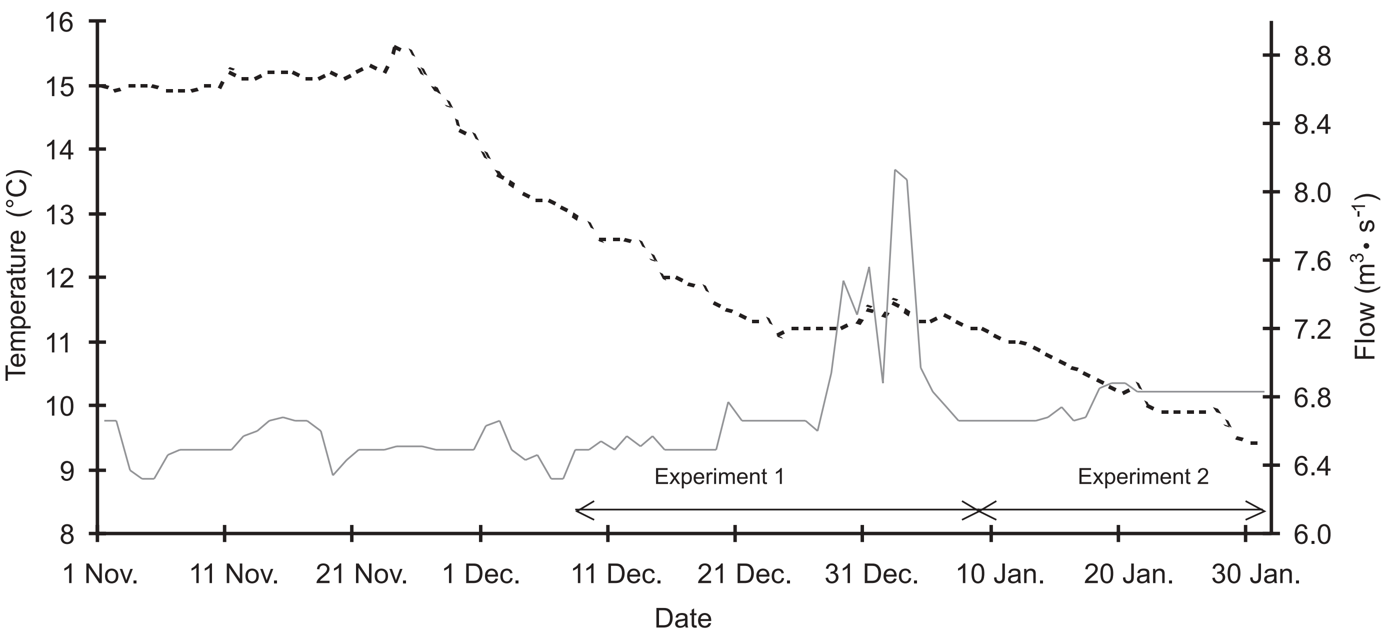
Chinook salmon embryos used to compare enhanced and unenhanced gravels were recovered on 8 January 2002, 28 days after egg-tube placement. Survival of chinook salmon

Table 2. Physical parameters associated with 10 egg tube monitoring sites and the Mokelumne River Fish Hatchery (control site)

					Peizometer measurements taken at time of egg-tube planting								
					Temperature (°C)			DO (ppm)			Permeability (mL·s^{-1})		
Site No.	DFCD[a] (km)	Water depth (m)	Stream velocity (m·s^{-1})	AT[b] (°C)	15 cm	30 cm	45 cm	15 cm	30 cm	45 cm	15 cm	30 cm	45 cm
Control	0.1			10.15	9.8			10.7			63		
1	0.8	0.3	0.65	10.10	9.8	10.0	10.2	10.2	7.7	6.1	38	41	28
2	1.4	0.2	0.78	9.97	9.6	10.0	10.0	9.9	9.5	9.1	42	17.5	9.25
3	1.7	0.2	0.67	9.79	10.3	9.8	9.8	9.2	6.9	5.9	40.5	14	25
4	1.8	0.2	0.75	9.88	10.6	10.1	9.9	8.0	8.2	8.5	41.5	19	16.5
5	2.3	0.2	0.75	10.11	10.1	10.0	9.7	10.3	10.1	10.1	35.5	9.25	5.5
6	6.3	0.2	0.89	9.73	9.8	9.9	9.8	9.3	8.5	6.9	44.9	43.6	32.5
7	7.1	0.2	0.65	9.79	9.9	9.5	9.5	9.6	7.3	6.4	44.8	42.5	35.5
8	8.5	0.4	0.96	9.87	9.5	9.5	9.6	9.2	6.4	6.1	44.1	23.85	8.5
9	9.5	0.3	1.02	9.61	9.4	9.1	9.2	9.2	7.3	7.1	47.6	12.5	1.2
10	10.5	0.3	0.65	9.72	8.7	8.7	8.9	9.0	8.1	7.2	18.2	21.5	11.5

Note: DFCD, distance from Camanche Dam; AT, average temperature in egg tubes at 15 cm; DO, dissolved oxygen; NTU, nephelometric turbidity

Fig. 3. Mean daily discharge rate and temperature of water released from Camanche Dam into the lower Mokelumne River from 1 November 2001 to 31 January 2002. The broken line indicates the temperature of the Camanche Dam release; the solid line indicates the rate of the Camanche Dam release.



embryos was highly variable. The chinook salmon embryo survival rate ranged from 0% in several unenhanced-gravel tubes to over 63% in tubes used as controls within the MRFH (Table 1).

Growth of chinook salmon was also variable. Chinook salmon embryos ranged from 11 to 31 mm TL in tubes incubated at the MRFH, while embryos incubated in river-gravel tubes ranged from 13 mm TL (site 3) to 30 mm TL (sites 4 and 5). Survival of chinook salmon alevins was significantly higher in enhanced gravel than in unenhanced gravel (Table 1; $t = 2.022$, df = 8, $P < 0.039$). No significant difference was observed for growth in enhanced and unenhanced gravel ($t = 0.038$, df = 8, $P = 0.485$).

Experiment 2: physical parameters associated with 10 spawning sites and their predictive power for salmonid survival and growth

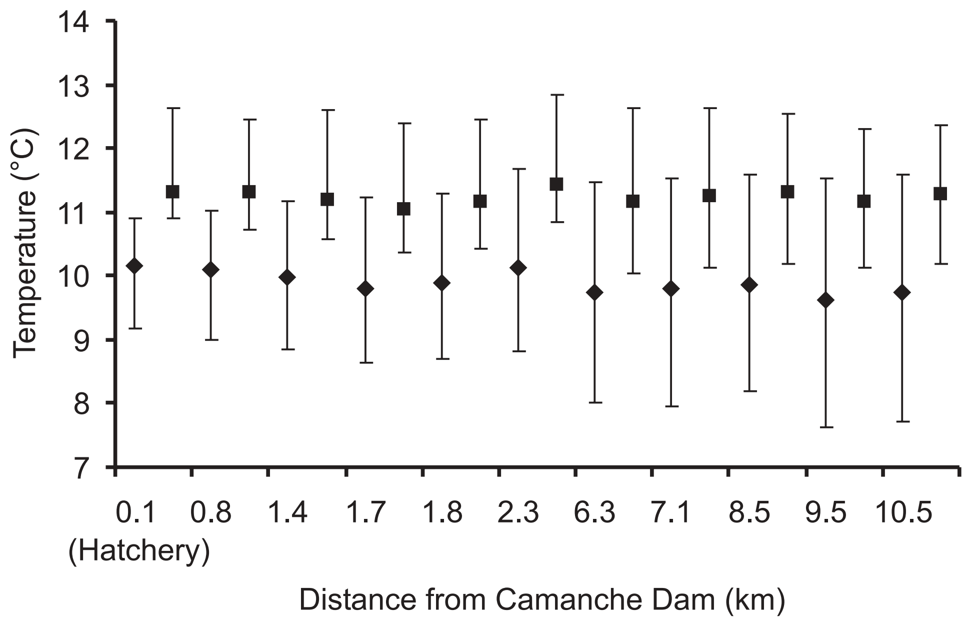
Camanche Dam releases to the LMR ranged from 6.6 $m^3 \cdot s^{-1}$ on 1 December 2001 to 6.8 $m^3 \cdot s^{-1}$ on 31 January 2002, with a peak of 8.1 $m^3 \cdot s^{-1}$ on 2 January 2002 (Fig. 3). Physical parameters associated with the spawning sites are provided (Table 2). Average daily temperature varied within the constructed redds. Although temperatures were somewhat consistent during experiment 1, during experiment 2, mean gravel temperature was inversely correlated with distance downstream of Camanche Dam (Fig. 4). Moreover, daily temperature variation was also greater downstream.

within the lower Mokelumne River, California, from 9 to 31 January 2002.

Turbidity (NTU)			TSS (mg·L^{-1})			VSS (mg·L^{-1})			d_{50} (mm)	
15 cm	30 cm	45 cm	15 cm	30 cm	45 cm	15 cm	30 cm	45 cm	Pebble count	Core
3.8			4.0			2.8				
24	1312	1024	14.6	362.4	809.7	6.3	61.8	122.4	385.6	370.5
970	1404	1328	297.2	547.8	573.3	30.1	59.2	73.9	423.3	455.5
24	1080	818	31.3	439.0	232.3	12.4	48.8	27.6	356.6	351.6
369	6137	4145	113.6	1150.7	1030.6	22.5	135.9	126.7	414.0	394.2
117	194	517	54.4	81.3	226.9	10.3	13.9	36.6	299.2	370.5
20	481	3050	32.3	365.6	1410.0	5.4	41.1	166.0	375.2	474.3
354	4450	3300	101.0	1504.7	465.7	18.8	175.3	57.3	203.7	159.2
18	369	374	55.1	226.1	577.0	6.3	25.8	67.9	251.5	314.6
343	378	1971	182.2	419.6	1194.0	28.6	48.9	95.0	203.4	74.1
696	1013	1180	177.0	377.6	471.1	25.0	46.8	59.5	152.2	156.7

units; TSS, total suspendeds olids; VSS, volatile suspended solids; d_{50}, median particle size.

Fig. 4. Temperatures recorded 15 cm below the gravel surface at 10 spawning sites and 15 cm below the water surface within the Mokelumne River Fish Hatchery (Hatchery). Average, minimum, and maximum hourly temperatures are shown for the monitoring period from 12 December 2001 through 8 January 2002 (experiment 1) (■) and for the monitoring period from 9 through 31 January 2002



Intergravel DO ranged from 6.1 mg·L^{-1} at 45 cm below the gravel surface to 10.11 mg·L^{-1} at 15 cm below the gravel surface. Intergravel permeability ranged from 1.2 mL·s^{-1} at 30 cm beneath the site 9 gravel surface to 48 mL·s^{-1} at 15 cm beneath the surface at the same site. We were able to draft 63 mL·s^{-1} through the standpipe in filtered hatchery water.

Spatial (i.e., distance from Camanche Dam) trends were observed in the variables collected (Table 3). As distance from Camanche Dam increased, average temperature within the gravels decreased and diurnal temperature fluctuations increased (Fig. 4). Surface substrate sizes, as indicated by pebble-count d_{50} (Pd_{50}) and general bed material size, as indicated by core-sample d_{50} (Cd_{50}), decreased as samples were taken farther from the dam. Correlations between turbidity, TSS, and VSS were strong, as were Cd_{50} and Pd_{50} measurements.

Chinook salmon and steelhead eggs used for the survival and growth models were recovered on 31 January 2002, 22 days after tube placement. Chinook salmon survival ranged from 0% to 100% in river gravel and from 74% to 98% within the MRFH. Similarly, steelhead survival ranged from 15% to 100% within river gravel and from 56% to 97% within the MRFH. Chinook salmon lengths ranged from 14 mm TL at site 5 to 25 mm TL within the tubes incubated at the MRFH. Steelhead lengths ranged from 13 mm TL at site 3 to 24 mm TL at all but two of the river sites. Chinook salmon and steelhead embryos tended to grow more slowly farther downstream from Camanche Dam, as indicated by average embryo size (Table 3).

While Cd_{50} and water depth appeared to have the strongest correlation with average rates of survival of chinook and steelhead embryos, respectively, no single physical parameter influenced both species strongly. The first four PCA axes explained over 87% of the total variance in physical conditions associated with the spawning locations (Table 4). The variables with the greatest loadings on each axis were distance from Camanche Dam, average VSS, and stream velocity.

Survival models

We used Cd_{50}, average VSS, and total temperature-hours as predictors of chinook salmon survival (Table 5A). The *F* ratio in the ANOVA for the overall model was significant at $F_{prob} < 0.01$ and the model accounted for 87% of the variation around the mean. We used average DO, temperature-hours, and average turbidity as predictors of steelhead survival (Table 5B). The *F* ratio in the ANOVA for the overall model was significant at $F_{prob} < 0.05$ and the model accounted for over 82% of the variation around the mean.

Growth models

We used temperature-hours, average permeability, average DO, and Cd_{50} as the independent variables to predict chinook salmon length at the time of egg-tube removal (Table 6A). The growth model accounted for 95% of the variation around the mean, with a significant *F* ratio for the ANOVA. We used Cd_{50}, average permeability, redd depth, and stream velocity as independent variables to predict steelhead length at the time of egg-tube removal (Table 6B). The growth model accounted for 89% of the variation around the mean, with a significant *F* ratio for the ANOVA.

Discussion

Growth and survival

Benefits documented for spawning salmonids and their developing embryos as a result of enhancement projects have been anecdotal, and typically inferred from measurements of physical habitat characteristics and observations of spawning activity (Zeh and Donni 1994; Van-Zyll-De-Jong et al. 1997). Our results indicate that LMR spawning gravel enhancements significantly increased chinook salmon embryo survival to swim-up stage up to 5 years after placement. Survival of salmonid embryos has been tied to DO (Coble 1961), temperature (Heming 1982), percent fines (Sear 1993), and permeability (Kondou et al. 2001) within spawning gravels. Merz and Setka (2004) showed that strategically placed gravel within the LMR significantly increased velocities and permeability, and decreased depths and fines, equilibrating the hyporheic and water-column environments, which supports our findings in this study. However, the short-term benefits of spawning-gravel enhancements may diminish through time if inter-annual bed mobilization from flushing flows is not provided (Wheaton 2003).

Although we observed no significant increase in embryonic growth in enhancement gravels during experiment 1, our preliminary egg-tube test showed a 24% average increase in survival and a 11% increase in growth of chinook salmon embryos placed in two enhanced sites when compared with two unenhanced sites in December 2000 (unpublished data). Embryo quality may have been a significant factor in the reduced benefits to growth observed in this study, considering that we observed 65%–100% survival in enhancement gravels in tubes buried for 4 weeks during our preliminary test and only 1%–67% within enhancement gravels during this study. Similar survival rates were also observed by hatchery staff monitoring the same egg lots incubated in the MRFH.

Physical correlations

The principal component correlations explain a few trends with respect to median grain sizes that are consistent with conventional geomorphic theory. First, surface bed material was consistently coarser than subsurface material. In gravel-bed streams, this is known as paving or armouring (Parker et al. 1982) and is thought to arise from differential erosion of coarse and fine grains in heterogeneous bed mixtures. Briefly, finer grains require less energy to erode than coarser grains, primarily because of their differences in mass. For example, a prolonged intermediate-flow event may produce hydraulic forces competent to erode fine- and medium-grained particles from the surface of a heterogeneous gravel bed, but not strong enough to erode the coarser grain particles. This, in turn, can lead to an armoured layer comprised of a higher percentage of coarse grains compared with a subsurface layer, which is not subjected to hydraulic forces adequate to winnow finer material away. Kondolf (1997) explains that, in regulated rivers like the LMR, surface armouring is often accentuated owing to flow-regulation conditions because larger particles that lag behind are less easily mobilized by hungry water below dams. Furthermore, dams block the passage of gravels, and once finer material (including spawning gravels) has winnowed away it is not replenished. Although the subsurface layers may provide a finite source of appropriately sized spawning gravels, they can become inaccessible or erodable under the protection of a coarse-armour veneer.

The second trend apparent in the principal component correlations is a reduction in grain size with distance downstream from Camanche Dam (fining). This fining of bed material is evident in both the surface median grain size and to a lesser extent the subsurface, consistent with the literature (e.g., Schumm and Stevens 1973; Ashworth and Ferguson 1989). Constantine et al. (2003) documented downstream fining in the gravel-bed reaches of the neighbouring Cosumnes River, but also noted the presence of a confined gravel-bed reach where downstream fining was not evident. They attributed the lack of decrease in grain size in that discrete reach to equal mobility of all bed material and incised channel morphologies that limit the freedom of the channel to migrate laterally. Given the incised nature of the LMR channel and the artificial reset of grain sizes at enhanced sites located throughout the LMR, one might suspect that the downstream fining trend would not persist in similarity to the Cosumnes River. However, the rather small percentage of the entire spawning reach actually covered by enhanced gravels (<2%) may prevent a noticeable influence on the general fining trend (Merz and Setka 2004). Furthermore, the equal mobility of all grain sizes observed in the Cosumnes River is in response to a nonregulated natural

Table 3. Principal component correlations among dependent and independent variables for chinook salmon and steelhead embryos developing in spawning gravel of the lower Mokelumne River from 9 to 31 January 2002.

	Physical variable											
Variable	DFCD	WD	SV	TH	TA	PA	DOA	TURA	TSSA	VSSA	PD_{50}	Cd_{50}
Chinook salmon												
CSSurvival	–0.273	–0.302	0.353	0.063	0.339	–0.257	0.113	–0.373	–0.386	–0.449	0.487	0.635
CSAS	**–0.721**	–0.412	–0.090	0.681	0.554	–0.466	0.495	–0.170	–0.418	–0.320	0.685	0.690
CSSM	–0.661	–0.244	–0.405	**0.794**	0.408	–0.136	0.491	–0.464	–0.665	–0.493	0.546	**0.708**
CSSMX	–0.600	–0.173	–0.110	**0.788**	0.500	–0.249	0.411	–0.158	–0.385	–0.226	0.614	**0.731**
Steelhead												
STHSurvival	0.108	–0.625	–0.171	–0.142	–0.133	–0.302	0.386	0.505	0.298	0.215	–0.116	–0.099
STHAS	**–0.710**	–0.629	0.006	0.511	0.634	–0.182	0.549	–0.122	–0.262	–0.247	**0.781**	**0.831**
STHSM	0.381	0.325	0.246	–0.087	–0.343	0.101	0.237	0.216	0.451	0.441	–0.124	–0.037
STHMX	–0.535	–0.188	0.327	0.563	0.565	–0.309	0.544	–0.395	–0.428	–0.424	0.498	0.528
Physical variable												
WD	0.651											
SV	0.423	0.429										
TH	**–0.753**	–0.208	–0.385									
TA	**–0.883**	–0.209	–0.391	0.608								
PA	–0.103	–0.016	–0.149	–0.052	0.356							
DOA	–0.410	–0.408	–0.104	0.572	0.247	–0.372						
TURA	–0.122	–0.494	–0.258	–0.162	0.273	0.344	–0.078					
TSSA	0.132	–0.169	0.143	–0.433	0.091	0.487	–0.215	**0.836**				
VSSA	–0.360	–0.214	–0.078	–0.221	0.224	0.586	–0.183	**0.880**	0.954			
Pd_{50}	**–0.863**	–0.592	–0.104	0.524	**0.866**	0.240	0.289	0.178	0.107	0.220		
Cd_{50}	**–0.724**	–0.509	–0.089	0.579	**0.757**	0.214	0.380	–0.022	–0.127	–0.003	**0.891**	

Note: Boldface type denotes correlations greater than 0.7. CSSurvival, average chinook salmon survival rate; CSAS, chinook salmon average size; CSSM, chinook salmon minimum size; CSSMX, chinook salmon maximum size; STHSurvival, average steelhead survival rate; STHAS, steelhead average size; STHSM, steelhead minimum size; STHMX, steelhead maximum size; WD, water depth; SV, stream velocity; DFCD, distance from Camanche Dam; TH, temperature-hours; TA, average temperature within gravel; PA, average gravel permeability; DOA, average dissolved oxygen content within gravel; TURA, average water turbidity within gravel; TSSA, average total suspended solids within gravel; VSSA, average volatile suspended solids within gravel; Pd_{50}, pebble-count d_{50}; Cd_{50}, core-sample d_{50}.

Table 4. Principal component loadings for the first four axes for physical conditions associated with 10 spawning sites within the lower Mokelumne River.

Characteristic	Axis 1	Axis 2	Axis 3	Axis 4
Distance from Camanche Dam	**–0.9280**	–0.1830	–0.0372	0.0344
Average ambient temperature	0.8790	–0.2220	0.0037	–0.2330
Temperature-hours	0.8780	–0.2210	0.0093	–0.2340
Core-sample d_{50}	0.8110	0.1470	0.4170	0.1830
Pebble-count d_{50}	0.7950	0.3620	0.3660	0.2090
Average dissolved oxygen concn.	0.6190	–0.1980	–0.3420	0.4270
Water depth	–0.5930	–0.4490	0.3800	–0.2980
Average volatile suspended solids	–0.1180	**0.9490**	–0.0025	–0.0313
Average total suspended solids	–0.3020	0.9060	0.0128	0.1710
Average turbidity	–0.0134	0.9030	–0.3450	0.0386
Average permeability	–0.0040	0.6330	0.4700	–0.4860
Stream velocity	–0.4250	–0.1610	**0.5580**	**0.6270**
Percent total variance explained	39.30	29.05	10.19	9.33

Note: Values in boldface type indicate the component with the highest loading on each axis.

Table 5. Statistics and associated multiple regression results for two models used to predict (A) chinook salmon and (B) steelhead embryo survival in Mokelumne River spawning gravel.

(A) Chinook salmon.					
Summary of fit	R^2	R^2 adj.	Root mean square error	Mean of response	Sum of weights
	0.8650	0.7975	0.0807	0.5723	10
Source	df	Sum of squares	Mean square	*F* ratio	Prob > *F*
Model	3	0.2503	0.0834	12.8116	0.0051
Error	6	0.0391	0.0065		
Corrected total	9	0.2893			
Effect tests	N_{param}	df	Sum of squares	*F* ratio	Prob > *F*
Core-sample d_{50}	1	1	0.1917	29.4346	0.0016
Average VSS	1	1	0.0934	14.3472	0.0091
Temperature-hours	1	1	0.0760	11.6651	0.0142
(B) Steelhead.					
Summary of fit	R^2	R^2 adj.	Root mean square error	Mean of response	Sum of weights
	0.8232	0.6818	0.0717	0.6139	10
Source	df	Sum of squares	Mean square	*F* Ratio	Prob > *F*
Model	4	0.1196	0.0299	5.8201	0.0402
Error	5	0.0257	0.0051		
Corrected total	9	0.1453			
Effect tests	N_{param}	df	Sum of squares	*F* ratio	Prob > *F*
Average DO	1	1	0.0373	7.2675	0.0430
Temperature-hours	1	1	0.0356	6.9339	0.0464
Average turbidity	1	1	0.0361	7.0257	0.0454
Average permeability	1	1	0.0072	1.4078	0.2887

Note: N_{param}, number of parameters; adj., adjusted.

flow regime with no major dams blocking the replenishment of sediment. Thus, the armoured surface substrates of the LMR may exhibit downstream fining through the coarse relic deposits left behind from the pre-regulation flow and sediment regime.

We also observed a strong correlation between water temperature and distance downstream from Camanche Dam, evident in both average temperature and temperature-hours. Preece and Jones (2002) observed a 3-week lag in and a 5.0 °C reduction of annual maximum daily temperature on Australia's Namoi River after construction of a dam. Similarly, Camanche Reservoir acts as an insulator, cooling water within the spawning reaches of the LMR during summer and fall. However, this pattern is reversed during the winter period, with water actually cooling farther downstream from the dam.

Correlations between physical and biological parameters

Substrate-size Cd_{50} was significantly correlated with chinook salmon survival and, along with temperature-hours and

Table 6. Statistics and associated multiple regression results for two models used to predict chinook salmon (A) and steelhead (B) growth in Mokelumne River spawning gravel.

(A) Chinook salmon.					
Summary of fit	R^2	R^2 adj.	Root mean square error	Mean of response	Sum of weights
	0.9472	0.9050	0.3162	20.6088	10
Source	df	Sum of squares	Mean square	F ratio	Prob > F
Model	4	8.9686	2.2422	22.4320	0.0022
Error	5	0.4998	0.1000		
Corrected total	9	9.4684			
Effect tests	N_{param}	df	Sum of squares	F ratio	Prob > F
Temperature hours	1	1	0.6773	6.7766	0.0481
Average permeability	1	1	3.2321	32.3358	0.0023
Average dissolved oxygen	1	1	0.3008	3.0094	0.1433
Core d_{50}	1	1	2.7874	27.8869	0.0032
(B) Steelhead.					
Summary of fit	R^2	R^2 adj.	Root mean square error	Mean of response	Sum of weights
	0.8857	0.7943	0.1825	21.1139	10
Source	df	Sum of squares	Mean square	F ratio	Prob > F
Model	4	1.2910	0.3228	9.6898	0.0142
Error	5	0.1665	0.0333		
Corrected total	9	1.4576			
Effect tests	N_{param}	df	Sum of squares	F ratio	Prob > F
Core d_{50}	1	1	0.5481	16.4557	0.0098
Average permeability	1	1	0.1379	4.1391	0.0976
Depth	1	1	0.0859	2.5776	0.1693
Velocity	1	1	0.0294	0.8815	0.3909

Note: N_{param}, number of parameters; adj., adjusted.

VSS, explained 86% of the variability in predicted survival. Likewise, growth regression equations for both chinook and steelhead included Cd_{50}. The mechanistic pathway of the Cd_{50} effect likely involved a relationship with permeability (Sowden and Power 1985). Interestingly, while we observed strong correlations between Cd_{50} chinook alevin survival and growth, Cd_{50} only appeared to be strongly correlated with steelhead growth, not survival. According to Chapman (1988), mean particle size is not as good an indicator of steelhead survival as for other salmonid species. Usefulness of mean particle size may be limited because gravel mixtures with the same geometric mean can have different size compositions. While our study design focused on survival of salmonid embryos within the hyporheic environment, the placement of eggs in a tube provided protection from physical impacts from all but the smallest substrates (<2.9 mm diameter). It is expected that Cd_{50} would have a direct egg-size-dependent effect on survival of eggs deposited directly in substrate. Likely, direct impacts related to substrate size include physical abrasion and crushing in the case of smaller gravel and interstitial space or, in the case of larger interstitial space, increased trauma due to currents and decreased cushioning. In a similar vein, egg size varies between salmonid species and even within species. Fecundity and egg size are inversely related in Pacific salmon and vary over latitudinal clines, with northernmost populations producing more but smaller eggs (Flemming and Gross 1990). Quinn et al. (1995) showed that there was a correlation between egg and substrate size for sockeye salmon (*Oncorhynchus nerka*), implying a selective effect of gravel size on egg size. Natural-selection effects on salmonid egg size can occur over decades and may be influenced by hatchery production (Kinnison et al. 1998). Independent of body size, there is little variation in egg size within populations of salmonids and we assumed that the egg sizes in our study were similar for each species for each experiment (Flemming and Gross 1990).

Development rates in sockeye and chinook salmon embryos are optimized for thermal regimes present within a given population's home spawning area, suggesting a genetic component that may vary between populations (Hendry et al. 1998; Kinnison et al. 1998). Although we used Feather River steelhead eggs, we assume that there is little difference between the present populations considering the high egg-importation rate by hatcheries over the past four decades (Bryant 2000). Even so, genetic influence on development rates should be considered when compiling information on restoration techniques and resulting salmonid physiological performance (growth, behaviour, mortality).

Intra-watershed variation must also be considered. For instance, the thermal shift in the LMR below Camanche Dam appears to affect embryo survival and growth. We observed both slower growth with cooling downstream of the dam late in the season and increased growth with warming earlier in the season (unpublished data). The reservoir insulating effect (i.e., warming water in winter and cooling water in summer and fall) will affect oxygen-saturation levels as well.

Numerous studies have documented correlations between individual physical parameters and embryo survival (Coble 1961; Heming 1982; Sear 1993). However, a specific action, such as increasing substrate permeability, may also influence temperature, DO, or even predator access to developing embryos. Shepherd et al. (1986) showed that the thermal mass of the substrate in Pacific Northwest coastal streams caused parallel but lagged and buffered heating and cooling trends in infiltration-source intergravel water compared with surface water. Similarly, this study and other work performed on LMR spawning gravel enhancement demonstrated that during the early portion of the fall-run chinook salmon spawning season (October through early November), intergravel water may be as much as 2.3 °C warmer than surface water, potentially influencing growth and development within the different embryo life stages. Salmonid egg to fry development is generally partitioned into three phases: prehatch, posthatch, and terminal phase. During the posthatch phase, yolk utilization increases markedly concurrently with increased somatic growth and organogenesis. The terminal phase is when the fish begins the transfer to exogenous feeding. It is during the terminal phase that suboptimal environmental conditions effects are manifested in either reduced physiological performance or increased mortality. Prior to the terminal phase suboptimal conditions generally affect growth rates and yolk-utilization efficiencies, whereas sublethal or critical conditions lead to developmental arrest and death. Progression of embryonic development is highly susceptible to regulation by extraneous factors such as temperature and DO, both of which are correlated with hyporheic flow (Chapman 1988). During the study period intergravel temperatures ranged from 7.6 to 12.8 °C, well within the optimal incubation range for chinook salmon and steelhead (Bjornn and Reiser 1991). Results from experiment 2 indicate that, as expected, temperature affected the growth and presumably the yolk-utilization efficiency of the embryos, but had no significant impact on survival. However, this study was performed during the middle of the LMR redd incubation period (October through April) and results could be different at either end of this period.

The use of several physical-parameter measurements to construct a predictive model of chinook salmon and steelhead survival and growth worked well. In addition to the parameters discussed above, VSS, DO, permeability, depth, and water velocities were all used in regression equations to predict growth and survival. While literature and previous work on the LMR support the fact that each of the parameters listed can influence salmonid physiology, their inclusion in our predictive model is not necessarily indicative of a significant effect individually (Garric et al. 1990). In our analysis we found that there were significant differences in the predictive power of regression equations based on what combination of parameters was used. While individually some parameters, such as average temperature, had a higher correlation with average steelhead size, when included in a suite of parameters they were not as useful as stream velocity in maximizing the predictive power of the regression equation. While the bulk of variation in growth and survival is explained by two or three parameters, the inclusion of minimally correlated measures may act to fine-tune equations to particular sites or systems. Leftwich et al. (1997) compared the predictive power of local and regional habitat models for the tangerine darter (*Percina aurantiaca*). Their results indicate significant differences in the relative importance of limiting factors between habitats, which limited the transferability of local-habitat models. It is likely that the influence of nonlimiting parameters in predictive models would also vary geographically, emphasizing the importance of collecting a full suite of data when evaluating restoration projects and the significant relatedness between some parameters (Koslow et al. 2002).

Management implications

It is important to note that the steelhead and chinook salmon embryos were not exposed to the test environment during their earliest development period. Even so, our results suggest that survival and development effects from manipulation of the spawning and incubation environment can be accurately measured. By increasing substrate porosity, hyporheic and surface water quality can be equilibrated. However, these synergistic effects greatly complicate evaluation of enhancement benefits, especially when parameters are assessed individually. These effects may explain documented low correlations between alevin survival and substrate-permeability measurements.

The simple test comparing embryo survival in enhanced and unenhanced gravels performed here provides some of the first evidence of short-term biological benefits of spawning-habitat rehabilitation. From a subset of the 12 parameters we were able to develop predictive multiple regression models for chinook salmon and steelhead embryo survival and growth, which suggests that benefits from gravel augmentation can be predicted and measured. However, this is not to suggest that all forms of spawning-habitat rehabilitation will or should yield similar improvements in embryo survival. Instead, there are logical explanations for differences between substrate conditions in enhanced and unenhanced gravels that may then explain the observed differences in survivability. The four spawning bed enhancement sites consisted of riffles constructed between 1994 and 2001. Unlike gravel augmentation or hydraulic structure placement forms of rehabilitation, these projects involve the direct placement of clean, optimally sized spawning gravels to form immediate spawning habitat (Wheaton 2003). On the LMR, typical fill depths of these projects are greater than egg-burial depths (>25 cm). Merz and Setka (2004) showed significant reductions in channel depth, sediment fines, and intergravel temperature and significant increases in stream velocities, intergravel permeability, and DO. Therefore, strategic gravel placement equilibrated the hyporheic and water-column environments and related positively to embryo survival rates. As Pasternack et al. (2004) point out, ad hoc implementation (as done on the LMR from 1991 to 2000) of spawning bed enhancement projects without a systematic design process (e.g., Wheaton 2003) can lead to less efficient gravel placement. To better gauge the benefits of such projects to the effort applied, we suggest appropriate cost-benefit analysis of material and effort in terms of actual embryo or fry production. Furthermore, while site-specific augmentation appears promising, it is important to note that the LMR is a relatively low gradient stream with a highly regulated flow. Using the methods presented here in other river systems should increase our understanding of how gravel-enhancement projects work in different situations. This understanding, in turn, can be linked to the establishment of healthy ecosystem, hydrologic, and geomorphic processes.

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