

ARTICLE

## Contrast of Degraded and Restored Stream Habitat Using an Individual-Based Salmon Model

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**Abstract**

Stream habitat restoration projects are popular, but can be expensive and difficult to evaluate. We describe inSALMO, an individual-based model designed to predict habitat effects on freshwater life stages (spawning through juvenile out-migration) of salmon. We applied inSALMO to Clear Creek, California, simulating the production of total and large (>5 cm FL) Chinook Salmon *Oncorhynchus tshawytscha* out-migrants at a degraded and a restored site. The calibrated model reproduced observed redd locations and out-migrant timing and size. In simulations, the restored site had a much higher production of fry that established and grew before out-migration; it provided higher survival and positive growth due to moderate velocities, shallow depths, and cover for feeding and hiding. The restored site did not produce more total out-migrants because at both sites spawning gravel was sufficient and the vast majority of fry moved downstream soon after emergence. Simulations indicated that at both sites increasing food and cover availability could further increase production of large, but not total, out-migrants; spawning gravel, temperature, and flow appear nearly optimal already. Further gravel addition was predicted to increase total fry production but have little or even a negative effect on production of large out-migrants, illustrating that actions benefitting one life stage can negatively affect others. The model predicted that further enhancements (e.g., in cover availability) would be more beneficial at the restored site than at the degraded site. Restoration efforts may be most effective when concentrated in “hot spots” with good habitat for growth and predator avoidance as well as for spawning. Contradicting the traditional notion of “limiting factors,” the model indicated that several factors each have strong effects. The model provided more understanding of restoration effects than would field studies alone and could be useful for designing projects to meet specific restoration objectives.

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Designing and evaluating fish habitat restoration projects are important yet difficult tasks for freshwater fisheries managers. There is limited guidance available for designing successful river restoration projects, in part because most completed

projects are either not evaluated or evaluations cannot clearly document success (Bernhardt et al. 2005; Roni et al. 2008; Jähnig et al. 2011). Many restoration projects are designed to create a perception of “good” habitat without addressing the root

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causes of degradation and ultimately fail to accomplish desired objectives (Beechie et al. 2010). In response, recent literature has outlined best practices for achieving positive restoration outcomes (Beechie et al. 2010; Bernhardt and Palmer 2011). One of the fundamental principles is to develop a process-based approach to restoration focused on restoring hydrologic, geomorphic, and biological processes that maintain river ecosystem function. An important step in this approach is to explicitly link potential management actions to restoration objectives by predicting the effects of alternative management actions on ecological processes and fish population response. At the reach scale, designing restoration actions that directly influence such processes as habitat selection, predation, feeding, growth, and competition can achieve positive outcomes for fish populations (Beechie et al. 2010).

Modeling restoration actions allows managers to clarify their objectives, define assumptions about the relationships between actions and ecological processes, explore sources of uncertainty, and quantify predicted outcomes. Once restoration projects are completed, models can be used to evaluate their effects on fish populations by integrating field data on multiple processes. In addition, models can be used as a decision-support tool by evaluating alternative restoration scenarios to determine actions that best achieve the fundamental objectives of a project, such as maximizing fish population response (Honea et al. 2009; Beechie et al. 2010; Stewart-Koster et al. 2010). Alternative scenarios can include type of management action as well as site selection, recognizing that the spatial context of a restoration site may have a large effect on the project outcome (Bernhardt and Palmer 2011). Use of models to evaluate completed projects or potential future restoration actions can encourage projects to be process-based, have quantifiable objectives, and be designed for modification through adaptive management.

The use of models in monitoring and evaluation of restoration projects has long been advocated. In fact, modeling is an integral part of adaptive management, as originally envisioned (Walters 1986; Walters and Holling 1990). While many managers think of statistical models that are fit to field data as the natural framework for adaptive management, simulation models have also been used in especially complex and prominent situations (e.g., Walters et al. 2000; Korman et al. 2011). Individual-based models (IBMs) are especially attractive for evaluation and adaptive management of restoration projects because they predict how meaningful population responses (e.g., number of successful offspring) arise from habitat effects that are most clear at the individual level and can integrate the cumulative effects of the multiple kinds of change made in restoration. Individual-based models can combine models of (1) the physical environment and how it is affected by restoration, (2) relevant physiological and behavioral processes strongly affected by the environment (e.g., feeding and growth, survival, spawning), and (3) key adaptive behaviors such as selecting habitat and deciding when and where to spawn. Individual-based models can be quite complex, which makes them nontrivial to build and apply, but they also

provide more potential for understanding the inherently complex effects of management on fish populations (e.g., Harvey and Railsback 2007; Railsback and Harvey 2011).

We introduce and illustrate the use of inSALMO, a new IBM designed to support management of freshwater life stages of salmon—spawning through rearing and out-migration. The model is adapted from a family of IBMs that have been applied to a variety of salmonid management and research issues (Railsback and Harvey 2001; Railsback et al. 2009; see [www.humboldt.edu/ecomodel/instream.htm](http://www.humboldt.edu/ecomodel/instream.htm)). We describe the model and its application to two sites that represent restored and degraded conditions in Clear Creek, a productive but highly modified salmon spawning stream in California's Central Valley. We use the model and field observations to contrast Chinook Salmon *Oncorhynchus tshawytscha* spawning, incubation, and juvenile rearing between the two sites. The analyses produced general conclusions about restoration and the model's usefulness.

## STUDY SITE

The location chosen for this demonstration application of inSALMO is the Lower Clear Creek Flood Plain Restoration Project, Shasta County, California. Clear Creek flows generally east from the coastal mountain range into the Sacramento River and has a watershed area of approximately 650 km<sup>2</sup>. Base flows at the site are mostly instream releases from Whiskeytown Dam, part of a large interbasin transfer system. Lower Clear Creek is a productive Chinook Salmon spawning stream (Yoshiyama et al. 2000); Whiskeytown Dam limits upstream passage but provides reliable base flows and moderate temperatures. The creek supports runs of steelhead *O. mykiss irideus* and fall, late-fall, and spring runs of Chinook Salmon. Fall-run Chinook Salmon dominate in our study sites; adults arrive mostly in October and spawn from October through November, with most juveniles migrating downstream as presmolts in their first spring and summer (Earley et al. 2010).

The lower end of Clear Creek was heavily disturbed by gravel mining such that much of the channel became narrow and steep with hard clay substrate instead of gravel. Several major actions have been taken to improve salmon and steelhead habitat. From 1995 through 2001, flow releases from Whiskeytown Dam were gradually increased from a median of 1.9 m<sup>3</sup>/s to 6.1 m<sup>3</sup>/s, with a consequent decrease in mean annual water temperature of 2.5°C. Since 1996, spawning gravel has been injected in several places for natural transport downstream. In 2000, a small dam at river kilometer (RKM) 10.4 (upstream from the confluence with the Sacramento River) was removed.

The Flood Plain Restoration Project ("restoration") that we focused on was constructed in 2002 under the Central Valley Project Improvement Act, which was intended to reduce effects of U.S. Bureau of Reclamation water projects on Central Valley fisheries. Restoration design objectives included reestablishing a system of alternating riffles, exposed bars, and

pools, establishing an active floodplain and coarse sediment transport, raising the bed to provide substrate of gravel and cobble instead of the underlying hard clay, and increasing the area of gravel suitable for spawning (NSR et al. 2000). This restoration project was an attractive study location because it offered contrasting sites with and without channel restoration and because the U.S. Fish and Wildlife Service (USFWS) (e.g., Earley et al. 2010) has extensively monitored variables such as spawner abundance, juvenile habitat use, and the redd location and out-migrant data we describe below.

We contrasted two study sites. The degraded site (designated “DEGRD”) was one of four used to represent prerestoration habitat (site 3C of Gard 2006). It is 460 m in length and has a mean wetted width of 14 m at base flow. The restored site (designated “RESTO”; Figure 1) was the first in-channel phase of restoration (site 3A of USFWS 2006). Prior to its restoration in 2002, the channel at RESTO had more bends and a lower gradient than DEGRD, but was similarly lacking in hydraulic complexity and shallow habitat. The restoration work recontoured parts of the channel, added structures such as log root wads to stabilize banks and provide cover, and added spawning gravel. The RESTO site is 490 m long and 27 m wide at base flow.

## MODEL DESCRIPTION

The model developed for this study is version 1.0 of inSALMO, adapted from an unpublished full-life cycle salmon model and the inSTREAM family of stream trout models. The inSTREAM models have been used for a variety of theoretical and management applications (e.g., Railsback and Harvey 2002, 2011; Railsback et al. 2003; Harvey and Railsback 2007, 2009). We provide an overview of the model here, focusing on processes that have not been published previously; a full description is provided by Railsback et al. (2012).

## Model Purpose

The model inSALMO is designed to help predict and explain the interacting, cumulative effects of river management actions on freshwater life stages of anadromous salmonids. Such actions include changes in flow, temperature, or turbidity regimes, alteration of channel shape and availability of spawning gravel and cover for feeding or hiding, and manipulation of biological conditions such as piscivorous fish densities and food availability.

## Entities, State Variables, and Scales

Version 1.0 of inSALMO represents habitat and fish in streams where adult salmon arrive from the ocean and spawn,



FIGURE 1. RESTO (Lower Clear Creek Flood Plain Restoration Project site 3A). This 2011 image (obtained from Google Earth) shows features of the 2002 restoration work: a wider and more sinuous channel, log structures for stability and habitat complexity in the bend at lower left, widespread spawning gravel, and a recontoured and replanted floodplain. [Figure available in color online.]

eggs and embryos incubate, and juveniles rear until they migrate downstream. The model can represent one or several species or races (“runs”) of salmon, each with their own parameter values. The model uses a daily time step.

Habitat is represented at two scales: reaches and cells. A “reach” represents a contiguous length of stream, typically several hundred meters in length. Simulations can represent one or more reaches, where fish move among them. Reach-scale habitat variables are daily flow, temperature, turbidity, and several parameters that determine how high flows affect spawning and the probability of redd scour.

Habitats within each reach are depicted as two-dimensional (depth-averaged) cells. Cells are irregular polygons, typically generated via GIS or hydraulic simulation software. Cells have variables for depth and velocity, calculated from flow using lookup tables generated using separate, standard, hydraulic models. The daily availability of drift food for fish is calculated from depth, velocity, and cell area. Availability of a second type of food (for “search feeding,” e.g., from the benthos) depends on cell area. Availability of these two food types also depends on parameters estimated via calibration (see Model Calibration and Evaluation section below). Cells also have static habitat variables that represent the amount of cell area that provides velocity shelters for drift-feeding and spawning gravel, and a characteristic distance to hiding cover. These static variables are typically evaluated via field observation. The assumption that velocity shelter area (e.g., provided by boulders, habitat structures, and banks) is independent of flow is an important simplification made to avoid additional complexity and uncertainty. Shelter area is typically observed during typical base flows, so this simplification should be reasonable most of the time, but perhaps not during high-flow events.

Salmon are represented by three kinds of model entity. “Adults” have state variables for sex and spawning status (whether they have spawned and, for females, whether they are guarding a redd) and length, which determines fecundity of females. “Redds” represent the nests of eggs, with a variable for the number of eggs remaining alive each day. “Juveniles” represent fish from emergence to out-migration, with variables for length and weight.

### Process Overview and Schedule

The following actions are executed each simulated day.

*Habitat updates.*—Daily flow, temperature, and turbidity are read in for each reach. Cell depth, velocity, and food availability variables are updated from flow.

*Adult arrival.*—Any adult salmon scheduled to arrive from migration (see Initialization section below) are placed in their spawning reach.

*Adult spawning.*—Adults decide whether they spawn and, if so, create a redd. An adult spawns if (1) it has not already spawned, (2) the date is within a range specified by parameters for each species or race, (3) the temperature is within a range specified by parameters, (4) the flow is below a maximum

specified as a habitat reach parameter and has not changed more than 20% from the previous day (so spawning does not occur when scour or dewatering are likely), and (5) a random number is less than a parameter we set to 0.2 (imposing a natural delay between arrival and spawning). However, adults always spawn if it is the last day in their range of spawning dates.

When a female adult spawns, it first identifies the best cell for spawning within a radius determined by its length (in this study, this radius typically includes an entire reach). (Adults are not allowed to move to a different reach to spawn because the number of spawners in each reach is an initial condition of the model, not an outcome of simulations.) The “best cell” has the highest value of a spawning suitability measure that considers depth, velocity, and area of spawning gravel not currently guarded by another female.

The spawning female creates a redd in the selected cell, and the number of eggs are a power function of spawner length (Healey and Heard 1984). The female then identifies a male to also spawn. Both spawners then have their weight reduced by 40% (Mesa and Magie 2006), which causes spawners to die of poor condition (below) within a few days (median lifespan after spawning = 7 d). The female’s spawning status variable is changed to “guarding.”

*Adult habitat selection.*—Female adults guarding a redd stay in the cell containing the redd. Male and unspawned female adults move to the cell offering the highest probability of survival (below), typically one with high depth (to reduce predation risk) and low velocity (to reduce energy costs and hence starvation risk, as adults do not feed).

*Juvenile habitat selection and out-migration.*—Juvenile salmon select and move to the cell within the radius in which they are assumed able to sense habitat conditions offering the highest “expected fitness,” a tradeoff between expected future growth and survival (Railsback et al. 1999; Railsback and Harvey 2002). The radius increases with fish length and always includes at least the adjacent cells.

Version 1.0 of inSALMO adds out-migration as a habitat selection alternative for juvenile salmon: if none of the available cells offer expected fitness higher than the expected fitness from out-migration, the juvenile abandons its reach and moves into the next downstream reach. When a juvenile decides to move downstream from the downstream-most reach, it is recorded as having migrated out of the system and removed from the model. A juvenile’s expected fitness from out-migration is represented simply as “relative out-migration success,” a logistic function of length (Figure 2) that reflects how the likelihood of successful migration to the ocean varies with length. Very small juveniles out-migrate only if expected fitness in their reach is very low, especially due to negative growth; as they grow, predation and other risks become more important. Larger juveniles remain in their reach only if growth is positive and survival probability is high (Figure 3).

*Growth.*—The daily change in weight is calculated from food intake and energy costs using a standard bioenergetics approach,

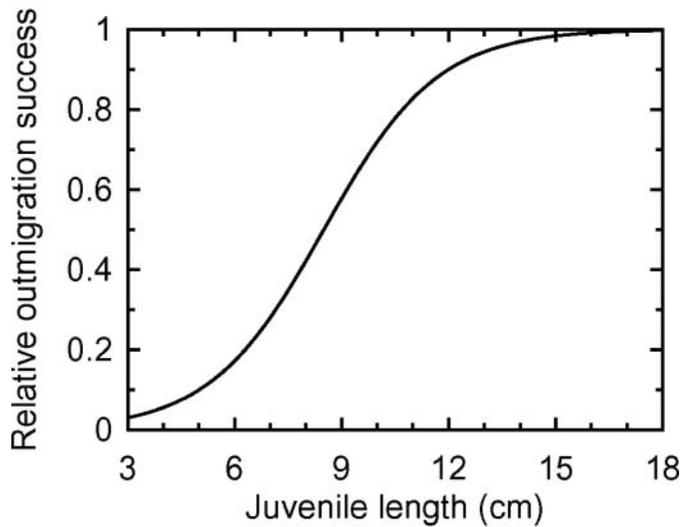


FIGURE 2. Relative out-migration success function for Chinook Salmon juveniles. The function's shape is controlled by two parameters: the lengths at which a juvenile's expected probability of surviving out-migration, relative to the maximum probability, is 0.1 (*fishOutmigrateSuccessL1*, 5.0 cm) and 0.9 (*fishOutmigrateSuccessL9*, 12.0 cm).

then added to the fish's previous weight. Because adults do not feed, their change in weight is always at least slightly negative. For juveniles, if the new weight exceeds the individual's previous maximum weight then an increase in length is based on an observed length–weight relation.

**Survival.**—Juveniles and adults are exposed to a variety of mortality risks that depend on both habitat and fish variables. Mortality due to poor condition (starvation and disease) becomes more likely as fish lose weight, which (for juveniles) often results from conditions such as low food intake and excessive velocities that cause high energetic costs. Juveniles are at risk of predation by other fish; this risk is lower if they use habitat that is shallow or close to cover. All but the smallest juveniles are also at risk of predation by terrestrial animals (e.g., birds, mammals), which can be reduced by selecting habitat that is deeper or closer to hiding cover.

**Redd survival.**—Survival of redds is modeled by determining how many eggs die each day due to dewatering (when a redd's cell is not submerged at the daily flow), scour and deposition (a function of flow, gravel size, and channel geometry), and temperatures either above or below optimal. Superimposition is modeled as a stochastic event that becomes possible when a redd is no longer guarded by its female and another female spawns in the same cell; the probability increases as the cell's area of unguarded spawning gravel decreases. Females neither prefer nor avoid superimposing redds. (inSALMO does not simulate effects of fine sediment on redd survival; doing so would substantially add to its complexity and uncertainty. Fine sediment is not believed to be a significant problem at Clear Creek.)

**Redd development.**—The daily increment in egg development is calculated from temperature using model 4 of Beacham

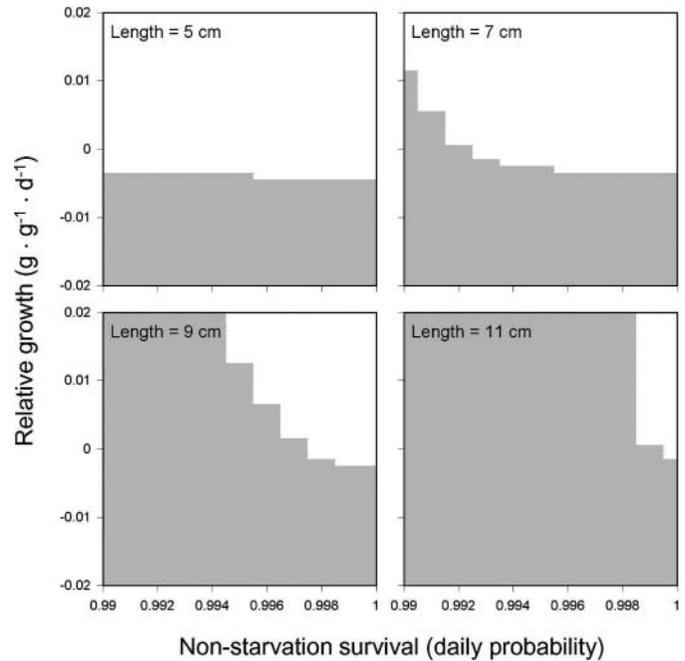


FIGURE 3. Results of the out-migration decision method with *fishOutmigrateSuccessL1* equal to 5 cm and *fishOutmigrateSuccessL9* at 12 cm. White regions indicate combinations of growth and risk conditions under which juvenile Chinook Salmon remain in their current reach, and grey regions indicate when they migrate downstream. The x-axis is the daily probability of surviving factors other than starvation (e.g., predation, high temperature). The y-axis is daily growth rate as grams of growth per gram of fish weight. The four panels show how results depend on fish length. Fish were assumed to currently be in good condition; lower condition (weight at length) slightly increases the tendency to migrate downstream. At lengths  $\leq 5$  cm, fish migrate downstream only if growth is negative. As length increases, out-migration becomes more dependent on risk; by 9 cm, fish migrate downstream if growth is more than slightly negative or if survival is not greater than about 0.995. By 11 cm, juveniles out-migrate unless survival is very high and growth is positive.

and Murray (1990). At constant temperatures, this model predicts eggs will develop fully in 94 d at 10°C and in 57 d at 15°C.

**Redd emergence.**—When a redd's eggs are fully developed, they “emerge” as new juveniles over several days. Juvenile length is drawn from a uniform distribution ranging from 3.5 to 4.1 cm fork length.

### Initialization of the Model

At the start of an inSALMO simulation, no fish or redds are present. Instead, a number of adult salmon are created and given dates at which they “arrive from migration” by being added to the model. Input for each species or race at each reach specifies the number of arriving adults, their sex distribution, the distribution from which individual lengths are drawn, and the distribution from which individual arrival dates are drawn.

### Superindividuals

The “superindividual” technique (section 7.9 of Grimm and Railsback 2005) is used to make simulation of dense spawning

populations computationally feasible. The model parameter *juvenileSuperindividualRatio* determines how many juveniles are represented by each juvenile object in the model. When redds emerge, the number of new juvenile objects is calculated by dividing the number of live eggs by *juvenileSuperindividualRatio*. The consumption of food and velocity shelter area of each juvenile object is then multiplied by *juvenileSuperindividualRatio*. No other changes in juvenile rules or behavior were made to implement superindividuals in the model. When a juvenile object “dies,” all the fish it represents die.

To determine the extent to which using superindividuals affects simulation results, we ran a sensitivity analysis on *juvenileSuperindividualRatio*, varying it from 1 (no superindividuals) to 100. Values of 10–20 were found to have negligible effects on the kinds of outputs we analyze, while greatly increasing computation speed. Here, we use a value of 20 individuals per object.

## METHODS

Our application of inSALMO to fall-run Chinook Salmon in Clear Creek had three steps: (1) assembling input for two study sites representing habitat with and without restoration, (2) calibrating and validating the model against field observations, and (3) designing analyzing simulation experiments to identify the differences between sites predicted by the model and why they occur.

### Input Data Assembly

*Hydraulic simulation.*—Hydraulic modeling methods for the DEGRD site are given in Gard (2006); similar methods were used for RESTO. The River2D two-dimensional hydrodynamic model (Steffler and Blackburn 2002) was used to simulate how depth and velocity vary over space and with flow. Transects placed at the top and bottom of each site provided an upstream water-surface elevation for calibration of River2D, the downstream stage–discharge relationship input to River2D, and part of the site bed topography. Additional bed topography plus substrate and cover data were collected using a total station, generally in sets of points going across the channel. Points were placed at changes in slope and to capture changes in substrate type and cover-related habitat. Bed topography data were collected in 2004 for RESTO and in 1999 for DEGRD. Bed topography, bed roughness, and substrate and cover distribution data were entered into River2D to create hydraulic models for each site. River2D was calibrated by adjusting bed roughness heights until simulated water-surface elevations matched measured elevations at the upstream transect. Hydrodynamic model predictions of stream velocity can be assessed by regressing them against observed velocities (e.g., Booker et al. 2001). For this purpose, a minimum of 50 velocity measurements were collected per site in addition to those collected at the transects. Results (USFWS 2005, 2006) showed strong correlation, indicating that velocity simulations are sufficient to represent the differences between sites that we address. Water-surface ele-

vations (and hence predicted depths) were generally accurate within 0.03 m.

*Habitat cells.*—We delineated habitat cells using GIS, starting with aerial photography of the site overlaid with the River2D mesh and habitat observations. Cell vertices were selected to capture important variation in habitat while producing no more cells than necessary. Consequently, cells tended to be small where habitat varied sharply with distance (especially along banks) and large in more homogeneous areas. This process produced 552 cells at the more complex RESTO site and 162 cells at DEGRD.

*Cell hydraulic and habitat variables.*—To model depth and velocity from daily flow, inSALMO input includes lookup tables of depth and velocity versus flow for each cell. The calibrated River2D models were used to simulate 24 flows at RESTO and 27 at DEGRD, ranging from below the lowest to above the highest recorded in Clear Creek during the period we modeled. Results of these hydraulic simulations were used to calculate depth and velocity in each inSALMO cell at each flow. Because the inSALMO cells are generally much bigger than the River2D mesh elements and laid out so that hydraulics are relatively uniform within cells, we calculated depth and velocity of a cell as the simple mean (not weighted by area) of values from all River2D nodes within the cell.

Cell-specific input on velocity shelters for drift feeding, distance to hiding cover, and area of spawning gravel was developed from field observations made March 23–25 and May 5, 2010. Velocity shelters and microhabitats providing hiding cover were relatively rare. We made point measurements of distance to cover and water velocity throughout both reaches in locations that allowed us to capture sharp gradients in these variables. In some areas, such as along stream margins where riparian vegetation provided both hydraulic complexity and cover for fish, point measurements were spaced every few meters and each point defined the velocity shelter and cover availability for a specific cell. Points were less dense in midchannel areas, where we made measurements specifically where rare habitat features provided velocity shelter or cover. We precisely located points with a Topcon Realtime Kinematic GPS (model R5). Spawning gravel was mapped onto aerial photos of the sites. Cover values for each cell were assigned in GIS as the field-observed value nearest the cell center; spawning gravel values were assigned by overlaying cells with the field-derived maps of gravel. Channel boundaries were also located during the 2010 field observations and compared with the River2D mesh in GIS to verify that channel shape had not changed substantially at either site.

*Adult numbers and characteristics.*—Spawner input specifies the number, characteristics, and timing of adult salmon arriving to spawn. Numbers of fall-run adults for each site were calculated from annual California Department of Fish and Game (CDFG) spawning escapement estimates for approximately 6.75 km of lower Clear Creek, which included both model sites. Adult numbers were produced by multiplying the total escapement estimate by the proportion of the overall reach

length represented by each model site. Input for adult sizes and sex ratio were generated from unpublished carcass data provided by CDFG.

### Model Calibration and Evaluation

After assembling input, we evaluated the model's predictions of where salmon spawn by comparing simulated versus observed redd locations, and calibrated its predictions of out-migrant timing and size by adjusting a few key parameters.

**Redd locations.**—Locations used for spawning have been observed at the study sites by mapping the extent of gravel that appeared disturbed by spawners during and after fall Chinook Salmon spawning in years including 2007–2010 (Giovannetti et al. 2008). These observed redd maps were overlain in GIS with the boundaries of inSALMO cells and then compared visually with redd locations in the inSALMO simulations. This approach allowed us to determine whether adults in the model spawned in the same general areas and the kinds of habitat that real spawners used, but has several uncertainties. First, the field observations are of a different type than the model results: the model predicts how many redds are in each cell, not the exact location or extent of redds, whereas the field observations attempt to delineate the extent of one or more redds. Second, there are potential errors in measuring redd extents and overlaying them with cell boundaries. Third, relatively high-quality spawning habitat is widespread at the study sites (especially RESTO), so exactly which cell an adult spawns in is partially stochastic (in the model and probably in reality). Therefore, we did not expect simulated redd locations to exactly match observations, but this analysis could illuminate any major errors in simulation of spawning location.

**Out-migrant timing and size.**—The main data-set available for calibration of inSALMO to the Clear Creek sites are rotary screw trap (RST) data collected by the USFWS (e.g., Earley et al. 2010) downstream from the study sites. The RST at RKM 2.7 is operated continuously during the juvenile Chinook Salmon out-migration period. Combined with mark–recapture studies conducted routinely to estimate trap efficiency, measurements of individual juveniles captured in the RST were used to estimate time series of numbers and size distributions of out-migrants.

The RST data had important limitations. First, the data were collected from the capture of out-migrating fish from the entire creek, not just our model sites; therefore, the RST data could not be used to distinguish between the study sites. Additionally, it was not clear how patterns in RST data were affected by differences between our two sites and the rest of the reach producing fry sampled by the trap (up to 4 km upstream from the model sites). Second, Clear Creek's spring and late-fall runs of Chinook Salmon could not be clearly distinguished in the RST data, making it difficult to discern a beginning or end of the fall-run out-migration that we simulated. Still, these data provided a useful view of how the number and size of out-migrating juveniles varied over time.

The model was calibrated by systematically varying five parameters that were particularly uncertain and affected the timing and size of out-migrants: drift food concentration (*habDriftConc*), search food production (*habSearchProd*), relative survival of predation by fish (*mortFishAqPredMin*) and terrestrial animals (*mortFishTerrPredMin*), and the out-migration success function (*fishOutmigrateSuccessL1*). The model was run for water years 2007–2009 using 360 combinations of these parameters. The parameter combinations were evaluated by how often (out of the 3 years) they met four criteria derived from the RST data: (1) the number of out-migrants with length > 5 cm should be above 10,000 per year from both sites, (2) out-migration should continue through at least June 1, (3) the date on which mean out-migrant length first exceeds 5 cm should be after April 15, and (4) the maximum daily mean out-migrant length should be between 6.5 and 8 cm.

### Simulation Experiment Design and Analysis

We simulated spawning, incubation, juvenile rearing, and out-migration of fall-run Chinook Salmon for five water years: 2004–2008. The analysis looked at differences between the two sites throughout these life stages, examining the number of eggs produced, egg survival, and the fate of juveniles—survival, growth, and timing of out-migration. When differences between sites were found, differences in habitat availability and use were examined for explanations.

In many analyses we distinguished between total out-migrants and out-migrants >5 cm in length (referred to simply as “large out-migrants”). Because the model assigns juvenile lengths of 3.5–4.1 cm upon emergence from redds, the 5-cm threshold is useful for distinguishing between juveniles that moved downstream almost immediately after emergence, most probably because they failed to find habitat providing positive growth (Figure 3, top left panel), and those that found productive habitat and grew at least a little before deciding to move downstream. Large numbers of Chinook Salmon fry moving downstream (voluntarily or not) immediately after emergence have been observed at many sites (Healey 1991), but the relatively few fry that grow significantly before out-migration may contribute disproportionately to adult returns. Miller et al. (2010) observed that 80% of the fish in a sample of Central Valley Chinook Salmon adults were longer than 5.5 cm when they encountered salt water as juveniles. This evidence is not surprising in California's Central Valley: a few kilometers downstream from our sites, out-migrants encounter increasingly large and warm water bodies where productive feeding conditions are probably rarer and predation risks greater.

### “Limiting Factors” Analysis

The inSALMO model includes a “limiting factors tool” that automates analysis of how sensitive the simulated production of out-migrants is to a variety of factors that could be affected by habitat management. These factors are: base flow, food availability, winter and summer temperature, spawning gravel

availability, velocity shelter for drift feeding, hiding cover, piscivory risk, redd scour, and the number of spawners. The tool sets up and executes simulations that vary these factors over ranges selected by the user and summarizes the response of key outputs such as the number of total and large out-migrants. The simulation experiments consider parameter uncertainty by running each limiting factor scenario multiple times using combinations of values for a few especially uncertain parameters. We used the limiting factors tool as a way of identifying and understanding effects of the habitat restoration and other potential management actions.

## RESULTS

### Model Calibration and Evaluation

**Redd locations.**—The comparison of simulated versus observed redd locations indicates that the virtual adults in inSALMO typically place redds in the same general locations as real salmon (Figure 4). The areas that real fish clearly avoid (e.g., the large bend at the west end of RESTO, both ends of DEGRD) are also avoided in the model. The areas of high model redd density, especially at RESTO, are similar to the large areas of observed redds. However, simulated redds at DEGRD are more widely distributed than the observed redds.

**Out-migrant timing and size.**—Of the four criteria developed from RST data for calibration of out-migration timing and size, the first, second, and fourth were robustly met across wide ranges of parameter values. However, the third criterion was rarely met; out-migrants > 5 cm length typically appeared one or several weeks earlier in the model than in the RST data. One set of parameter values was selected as best meeting all four criteria and being typical of the many combinations that met criteria 1, 2, and

4. These values are:  $habDriftConc = 0.001 \text{ g/m}^3$ ,  $habSearchProd = 0.008 \text{ g/m}^2$ ,  $mortFishAqPredMin = 0.94$ ,  $mortFishTerrPredMin = 0.98$ , and  $fishOutmigrateSuccessL1 = 5.0 \text{ cm}$ .

Using these calibrated parameter values, the model's out-migration timing was compared with the RST data by overlaying graphs of weekly numbers of out-migrants in the (1) RST and (2) model results (Figure 5). Peaks in out-migration correspond well, typically occurring in mid-February for both the model and the RST. However, out-migration from the model reaches begins later and ends earlier than out-migration at the RST. Model out-migration begins in mid-January while the RST data reports early December as the beginning of fall Chinook Salmon out-migration. Model out-migration becomes rare by the end of June, while in some years the RST continues to catch small numbers of Chinook Salmon identified as fall-run fish as late as September.

The size of simulated out-migrants was compared with the RST data (Figure 6). The model generally predicts the start of out-migration by large juveniles to be one to several weeks earlier than observed in the screw traps. The model reproduces the range of out-migrant sizes relatively well, which is not surprising: the smallest out-migrant size is determined by parameters for fish size at emergence, which were based on observations of real Chinook Salmon fry, and the largest out-migrant size was considered in calibration. However, the model also closely reproduces patterns in out-migrant size that are not closely imposed by model parameters: how out-migrant size (1) is constant at a low value for a number of weeks, then (2) rises sharply for a few weeks, (3) levels off or even dips in April, and finally (4) continues to increase as the last few out-migrants leave.

### Simulation Experiments

This section presents results of simulation experiments contrasting the degraded and restored sites. All statistics and figures present simulation output, not field observations.

**Egg production and survival.**—The inSALMO results indicated that spawning and incubation were equally successful at the two sites. At both sites and in all years, almost all (>94%) females produced redds. Survival to emergence was relatively constant among years and sites (across years, the mean and range at RESTO was 46% and 41–50%, respectively, and at DEGRD was 48% and 39–59%). Superimposition was the only major source of egg mortality, causing 50% loss (range among years, 44–54%) at RESTO and 48% loss (range, 41–50%) at DEGRD. Egg mortality due to excessively low or high temperature and associated disease was similar between sites because both were exposed to the same temperatures. No eggs were lost to either dewatering or scour; this was due in part to the upstream reservoir, so extreme high or low flows are rare. While our simulations did not include scour-inducing flows, the redd scour function in inSALMO (from Haschenburger 1999) predicted that widespread scour should be much less frequent at RESTO than at DEGRD, because of RESTO's wider and less-steep channel.

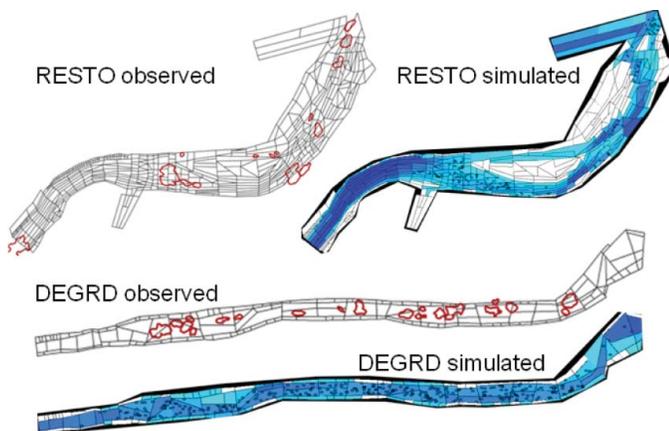


FIGURE 4. Comparison of observed and simulated redd locations for an example year, 2009. Observed redd extents are indicated by their curved boundaries. Simulated redd locations are indicated by the ovals placed randomly in the redd's cell, and cells are shaded progressively darker as depth increases (darker = deeper, white = not submerged). Redds extending outside the polygonal model cells are probably indicators of error in observing or overlaying locations, or of changes in channel shape since the model's topographic data were collected in 2004. [Figure available in color online.]

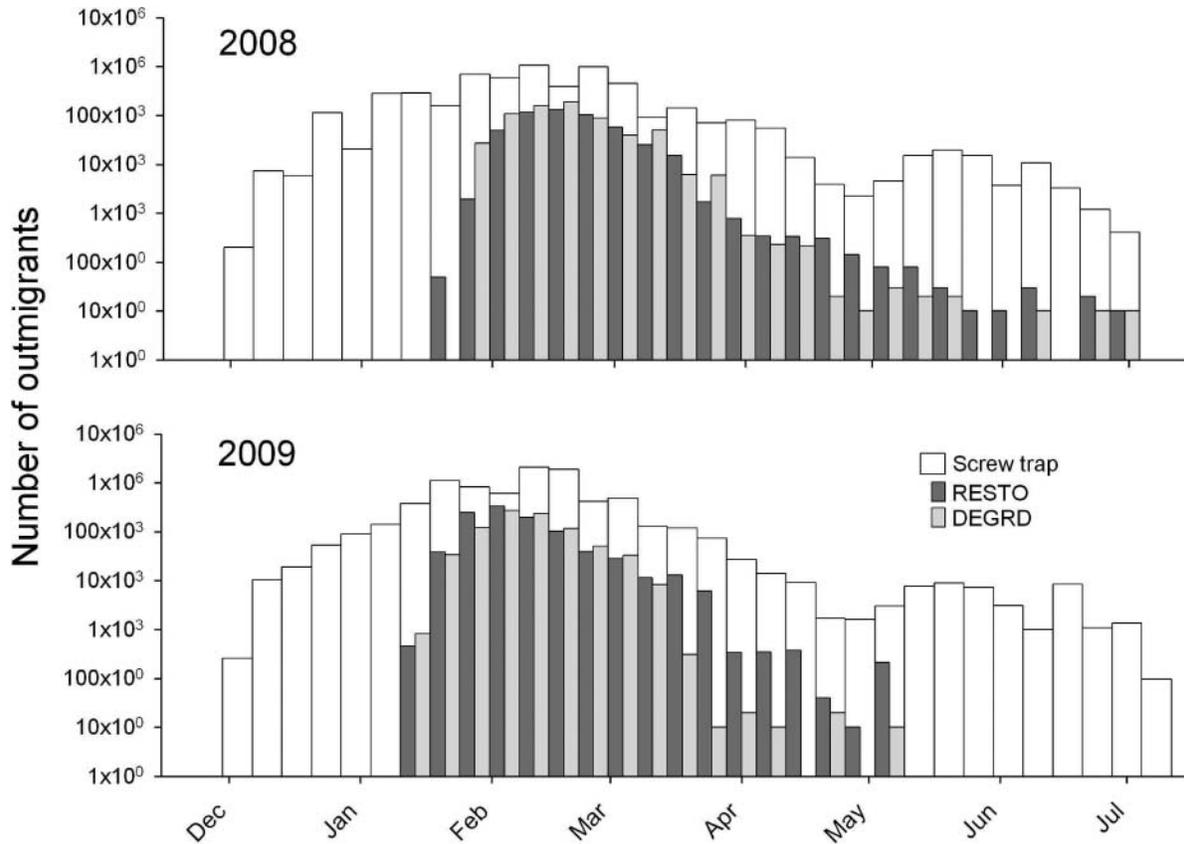


FIGURE 5. Out-migration timing results for water years 2008 and 2009. The y-axis is the number of out-migrants per week either observed at the RST and determined to be fall Chinook Salmon (wide white bars), or in the simulation (grey bars). Simulated out-migrants are separated by their reach of origin, indicated by dark (RESTO) and light (DEGRD) grey.

The similarity between sites in superimposition rates may seem unexpected because one purpose of the restoration project at site RESTO was to increase the availability of high-quality spawning habitat. However, the model input indicated that such habitat was almost equally available at the two sites at the time it was observed in the field. At a typical winter base flow of  $7.5 \text{ m}^3/\text{s}$ , the simulated area of spawning gravel with suitability  $> 0.5$  for both depth and velocity was  $2,900 \text{ m}^2$  at RESTO and  $2,500 \text{ m}^2$  at DEGRD, or  $5.8$  and  $5.5 \text{ m}^2/\text{m}$  reach length. Because the channel at DEGRD is much narrower than at RESTO, this means a higher percentage of area is suitable spawning habitat at DEGRD.

*Juvenile fates.*—At the juvenile and out-migrant stages, the simulations produced large differences between sites. The two sites produced approximately the same total number of out-migrants per spawner, but the number of large out-migrants was much higher at the restored site, RESTO (Figure 7). Of the relatively few juveniles that died before migrating downstream,  $>95\%$  of mortality was due to three causes. Predation by fish and terrestrial animals accounted for most mortality ( $88\%$  of mortalities at RESTO and  $75\%$  at DEGRD). Poor condition (due to rapid or persistent weight loss) was twice as common

at DEGRD ( $20\%$  of mortalities versus  $9\%$  at RESTO). The number of juveniles that died at RESTO was much higher than at DEGRD ( $43,500$  versus  $14,500$  over the entire simulation) simply because far more fish remained at RESTO for more than 1–2 d.

We further addressed the question of why RESTO produced many more large out-migrants by turning on inSALMO's optional output file that reported the habitat characteristics and fish fitness variables for each fish, each day, after the fish had selected the best cell available to it. We analyzed these results for all juveniles; the vast majority of these were newly emerged fry unsuccessfully seeking productive habitat near the cell containing their redd and, for site DEGRD, fish entering the reach at its upstream end after migrating downstream from RESTO. This output allows examination of the habitat conditions fish were able to find in their reach and the growth rates and survival probabilities they experienced as a consequence. These results emerged from (1) the model's assumption that fish seek, over a distance limited by their size, habitat offering positive growth and high survival, and (2) simulated habitat characteristics (depth, velocity, velocity shelter, hiding cover) near where juvenile salmon emerge from redds. For example, the

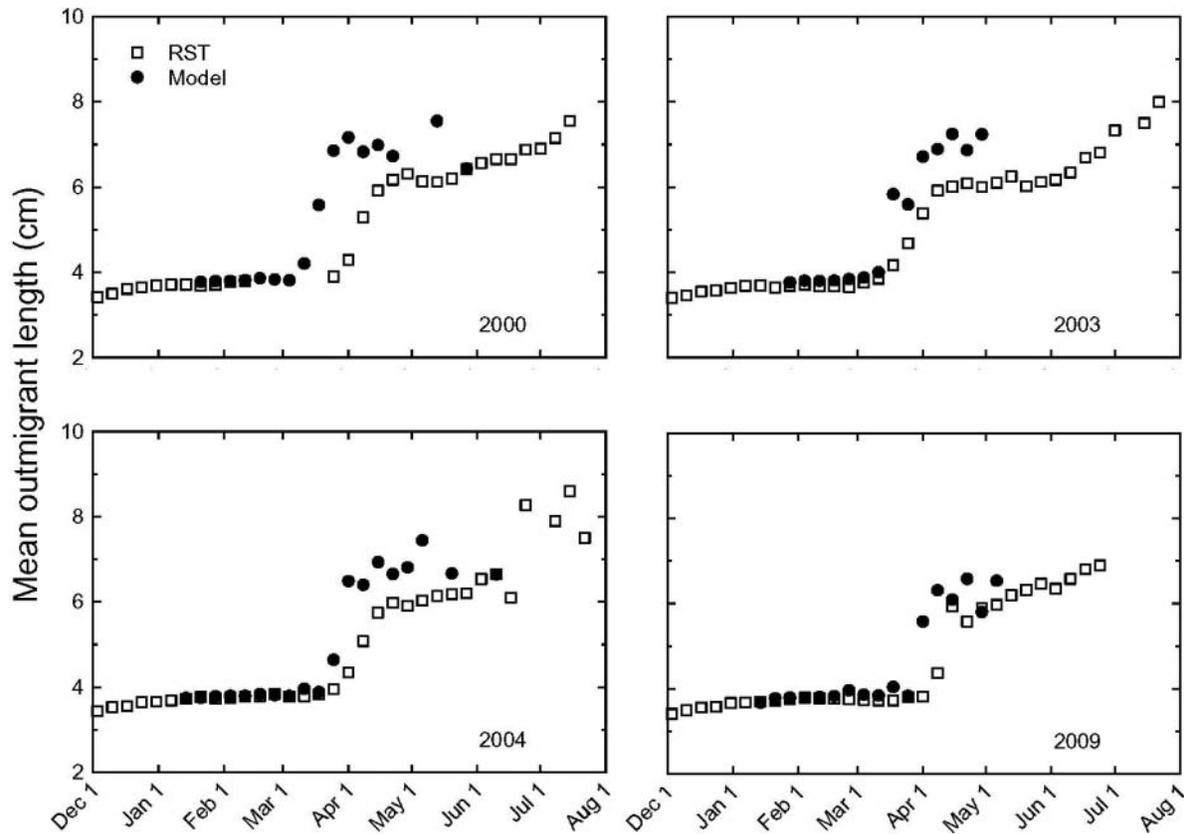


FIGURE 6. Out-migrant size calibration and validation results. The x-axis is the start of the week over which data are averaged. The y-axis is mean length of out-migrating Chinook Salmon. For four example years (2000, 2003, 2004, 2008), RST data are compared with calibrated simulation results.

distribution of cell depths and velocities used by juveniles (Figure 8) indicate that many juveniles, especially at DEGRD, were not able to find moderate velocities (where growth should be highest). At DEGRD, more juveniles used shallow depths where risk of being eaten by other fish was lower.

Compared with fish in the degraded reach, juvenile salmon in RESTO occupied habitat with higher levels of velocity shelter and hiding cover. At RESTO, juveniles used velocity shelter to reduce their swimming speed 20% of the time, compared with only 4% at DEGRD. Many more juveniles occupied cells with distance to hiding cover low enough to reduce predation risk at RESTO. Median distance to hiding cover was 1.5 m at RESTO, compared with 4.0 m at DEGRD; inSALMO's survival parameters assume this distance must be less than  $\sim 1$  m to reduce risk substantially.

These habitat differences produced substantial differences between sites in juvenile growth and survival potential (Figure 9). Even though differences between sites in net energy intake (Figure 9, left panels) appear small, the percentage of simulated juveniles experiencing positive net energy intake (weight gain instead of loss) was 38% at RESTO and only 18% at DEGRD. Juveniles more often obtained high survival probabilities (e.g.,  $>0.98$ ) at RESTO (Figure 9, right panels).

Another potential explanation for the higher production of large out-migrants at site RESTO is simply that RESTO is upstream from DEGRD. Before being recorded as out-migrants, juveniles spawned in RESTO move downstream through DEGRD, where they could find productive habitat and grow; juveniles spawned in DEGRD do not have another reach downstream to provide a second opportunity for growth prior to emigration. To test this explanation, we ran the experiment with sites reversed; a major reduction in large out-migrants from RESTO when it is downstream would confirm the explanation. Putting RESTO downstream from DEGRD did reduce the production of large out-migrants from RESTO but only slightly, from 0.95% to 0.83% of all out-migrants. Production of large out-migrants spawned at DEGRD more than tripled—from 0.14% to 0.48% of all out-migrants—when they migrated through RESTO. This result corresponds with the explanation that differences in juvenile growth are due to habitat differences between the sites, not their relative locations.

#### Limiting Factors Analysis

The limiting factor analysis indicated that the total number of out-migrants at DEGRD could be affected by the availability of spawning gravel (Figure 10, upper panel). While addition of

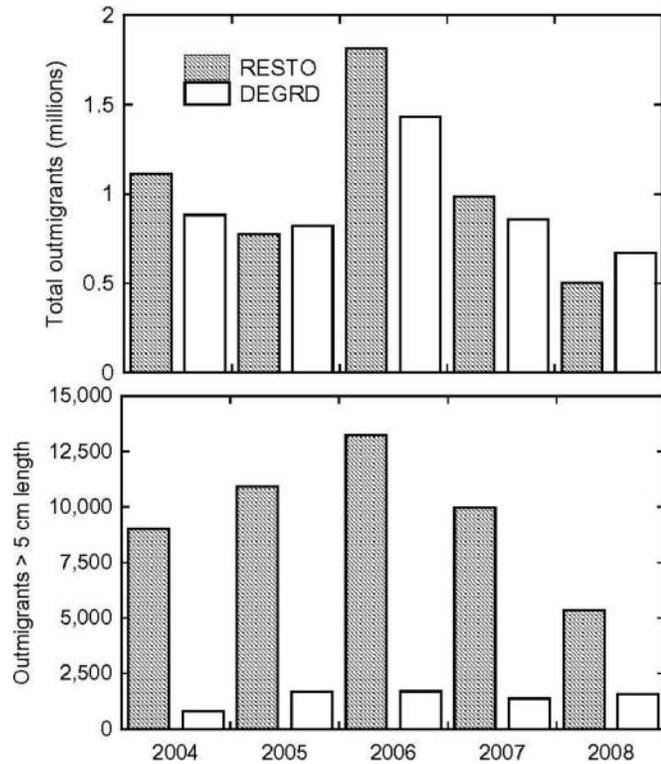


FIGURE 7. Number of total (top panel) and large (length > 5 cm; bottom panel) Chinook Salmon out-migrants in the habitat restoration analysis, by water year and site.

more than the baseline (actual) gravel area ( $x$ -axis > 0) had little benefit, reducing gravel area strongly reduced total out-migrant production at DEGRD. The mechanism for this effect was higher loss of eggs to superimposition when gravel is below baseline levels. The response of large-out-migrant production to gravel availability was small but opposite that of total out-migrants (Figure 10, lower panel).

The number of large out-migrants was most affected by food availability. The simulated response to food availability typifies the response to factors expected to have unambiguously positive effects on juvenile survival and growth (availability of velocity shelter and hiding cover, in addition to food). These factors had essentially no effect on total numbers of out-migrants (Figure 11, upper panel) because the vast majority of juveniles left within a day or two after emergence. However, they clearly increased the numbers of large out-migrants at both sites (Figure 11, lower panel). This positive effect (of velocity shelter and hiding cover, as well as food availability) was much more beneficial at RESTO because of the restored site's higher productivity of large juveniles. For example, a 100% increase over baseline food availability increased the percentage of out-migrants that were large by about 100% at RESTO and 190% at DEGRD, but the number of large out-migrants increased by 6,800 per year at RESTO and only 1,400 at DEGRD. Even though the mass of additional food was the same between sites, the higher area of good feeding habitat at RESTO allowed much more of the food to be captured and turned into growth by juvenile salmon.

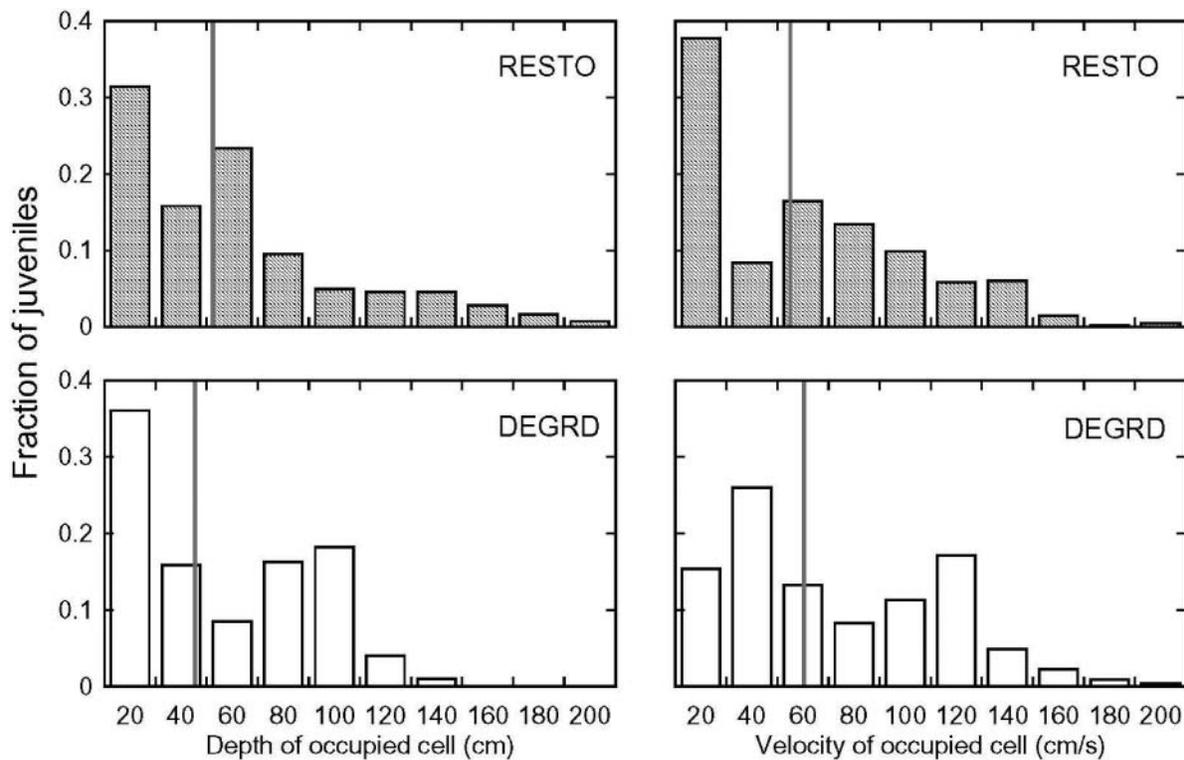


FIGURE 8. Distributions of cell depth (left panels) and velocity (right panels) for juvenile Chinook Salmon occupying the restored site RESTO (top panels) and degraded site DEGRD (bottom panels). The y-axis is the fraction of juveniles occupying cells with depth in the  $x$ -axis bin range (0–20, 20–40 . . . up to 180–200). The grey vertical line represents the median occupied depth or velocity.

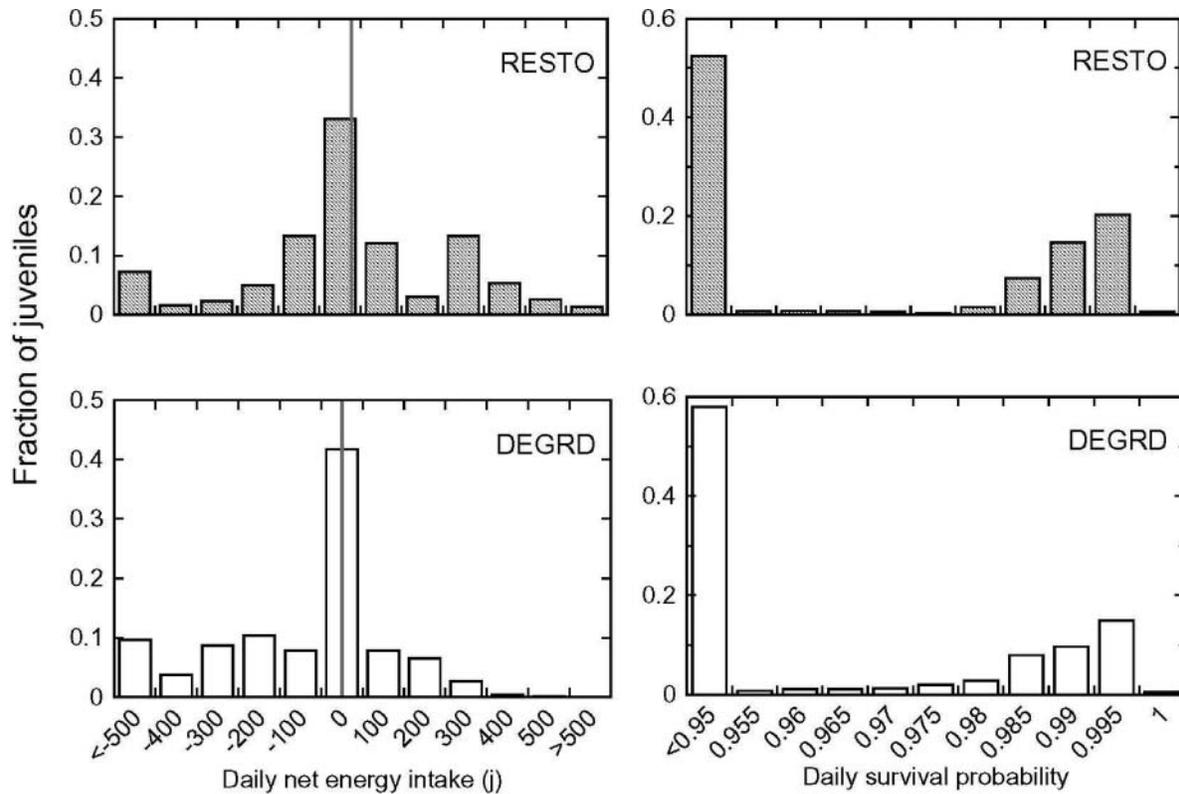


FIGURE 9. Differences between sites in Chinook Salmon juvenile fitness variables; format as in Figure 8. Left panels: histograms of daily net energy intake, i.e., the difference between energy intake from food and expenditure on metabolism and swimming; fish only grow if this variable remains above zero. Right panels: daily probability of surviving mortality sources other than starvation. Low survival probability values (e.g.,  $<0.95$ , at which expected lifespan is less than 14 d) often resulted from occupying cells with a velocity above the fish's maximum sustainable swimming speed (median survival was 0.013 at RESTO and  $2.0 \times 10^{-6}$  at DEGRD).

## DISCUSSION

### Modeling in Habitat Restoration Design and Evaluation

Evaluation of river habitat restoration projects is important but complex and difficult (Bernhardt et al. 2005). Conclusive evidence for the value of restoration projects, or relative value of alternative restoration designs, is very difficult to develop from field studies alone because of the many interacting processes and uncontrollable variables. Detailed, mechanistic models such as inSALMO contain many uncertainties that should not be neglected, and the credibility of the model's absolute predictions is not yet clear. However, these models are, at the least, useful for (1) providing a comprehensive framework for identifying, documenting, and linking information and assumptions, (2) exploring the consequences of such information and assumptions, (3) producing hypotheses for what processes and variables are important that can then be tested in the field, and (4) investigating relative differences among alternative management actions. Habitat assessment approaches, whether based on habitat selection (e.g., PHABSIM; Bovee 1982) or feeding and energetics (e.g., Hayes et al. 2007), are not as useful for such purposes, largely because they do not predict kinds of results (e.g., timing of emergence and out-migration, numbers

and sizes of fish) that are of direct management relevance and testable against field observations. Mechanistic models such as inSALMO are currently the only tools we have for forecasting the benefits of alternative restoration designs (and even basin-wide restoration strategies) that affect multiple factors such as physical habitat, food and cover availability, temperature, and flow.

While we studied a completed restoration project, models like inSALMO can also be used to support restoration planning decisions. Analyses like our "limiting factors" experiments can be useful for prioritizing management actions; our analysis, for example, indicated that further modifying base flow or temperature either up or down would have small or even negative effects. For channel reconstruction projects, simulation experiments can both compare alternative designs and evaluate the relative benefits to juvenile salmon production of details such as providing more gravel versus more hiding and feeding cover. This is in contrast to other approaches and guidelines for designing restoration projects (e.g., the spawning habitat restoration design process of Wheaton et al. 2004, and other approaches reviewed by Wheaton et al. 2004), which do not predict such specific biological responses. Previous approaches predict, at most, changes in "suitable" habitat area.

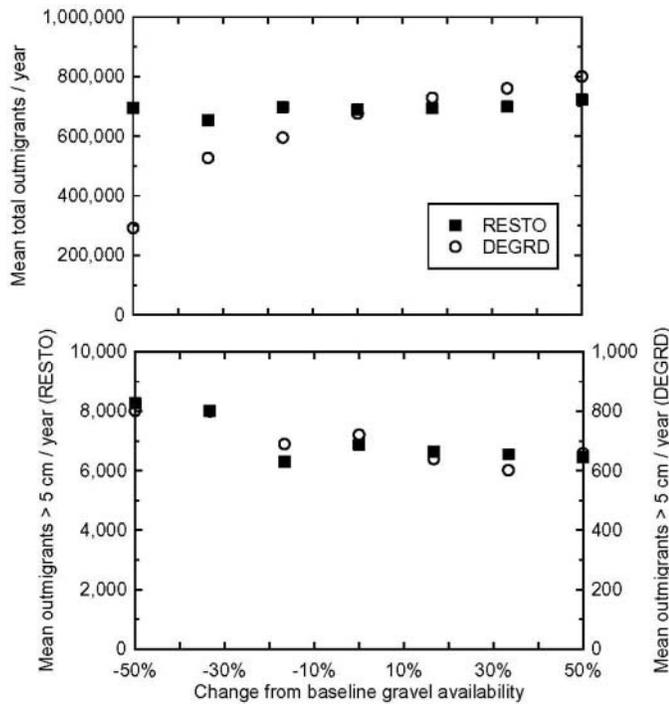


FIGURE 10. Limiting factors analysis results for spawning gravel. The x-axis is the percentage by which spawning gravel availability was changed from the observed value for each sensitivity scenario. The y-axis values are the mean of nine simulations using all combinations of low, medium, and high values of two uncertain parameters: food energy density and *fishOutmigrateSuccessL1*. The upper panel reports total number of Chinook Salmon out-migrants. The lower panel reports large (length > 5 cm) out-migrants, with separate scales for sites RESTO (left y-axis) and DEGRD (right y-axis).

Our continuing research objectives include testing inSALMO against more kinds of data collected at Clear Creek and evaluating how results depend on the total area and number of sites. The goal of this research is to determine whether and how the model can be used to support large-scale watershed restoration decisions.

### Evaluation of the inSALMO Application to Clear Creek

Our inSALMO simulations reproduced several key observations that were not imposed by assumptions or parameter values. Most important is the observation from RST data that the vast majority of juvenile Chinook Salmon move downstream as newly emerged fry instead of staying and growing before out-migration. Emergence of other patterns in out-migrant size and timing in the model give us some confidence in its predictions of growth and out-migration.

Some model results did not closely match monitoring data. Especially at site DEGRD, the model predicted redds to be distributed over more area than that observed. This difference could be reduced by adjusting the parameters for redd defense area or adult mortality (so spawners die sooner and, hence, defend redds for less time). However, the difference could also result from (1) spawning gravel being more widespread during

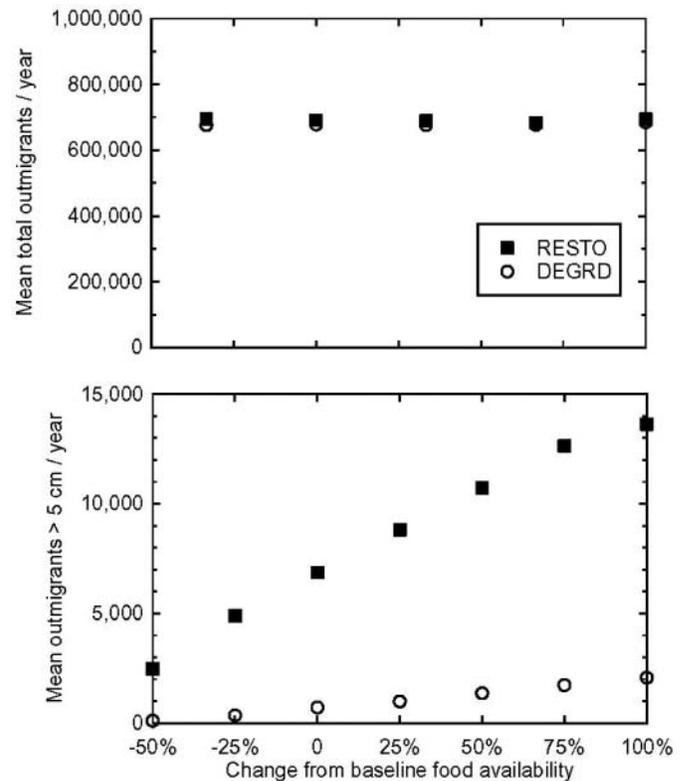


FIGURE 11. Limiting factors analysis results for availability of food for juvenile Chinook Salmon. The format is similar to that of Figure 10, except that both sites are represented on the left y-axis of the lower panel.

input data collection in 2010 than it was in previous years, perhaps due to the ongoing injection of gravel as part of the Clear Creek restoration program, (2) spawners being less attracted to DEGRD, violating the assumption we used in preparing input, that spawner density is constant over stream length, or (3) factors such as intragravel flow that affect spawning habitat quality but are not in the model.

The model also predicted out-migration to occur over a narrower range of dates than indicated by the RST data. In inSALMO, the timing of out-migration for the vast majority of juveniles who leave as newly emerged fry is strongly determined by the input defining when adults arrive and spawn and by the equation for how egg development varies with water temperature, which are all relatively certain. Hence, these discrepancies probably result from the RST collecting out-migrants from much more stream length and more kinds of habitat than represented by the two inSALMO reaches, and from uncertainties in distinguishing fall Chinook Salmon from other runs in the trap data.

One seemingly counterintuitive result from the limiting factors analysis was that further addition of spawning gravel could reduce the production of large out-migrants. The most likely mechanism explaining this result is that more gravel produces more emergent fry and, hence, greater competition and lower

growth. We commonly see negative relations between abundance and growth in inSALMO, due to competition for good feeding sites.

This application also identified several potential effects of restoration that the current version of inSALMO does not address. One is the effect of gravel quality on both spawning habitat selection and redd survival. Defining useful, quantitative measures of gravel quality and modeling them is complex and uncertain, and we simply chose not to add these uncertainties to the model. Second, we did not model how habitat differences among reaches affect which reach adults spawn in; instead, we simply specified how many adults used each reach. A straightforward approach for adding this process is to assume no inherent “site fidelity” at the reach scale and let adults select the best available habitat among multiple reaches when they spawn. Third, many of our key results concern the ability of newly emerged fry to find and occupy productive and safe habitat. The inSALMO model does not represent this process in detail; it neglects processes such as being swept downstream as passive drift and changes in swimming ability as fish complete their development from alevin to fry stages. The model’s predicted number of large out-migrants is in fact sensitive to its parameters controlling the radius over which fish can find habitat (Railsback et al. 2012, section 4.4.2).

### Contrast of Degraded and Restored Sites

This study did not directly evaluate the restoration project by simulating the RESTO site before and after restoration, but our comparison of RESTO to the degraded site provides useful inferences. The analysis indicates that RESTO was much more productive for larger juvenile Chinook Salmon than was the unrestored DEGRD.

Why did the model predict that far more fry remain and grow at RESTO than at DEGRD? One reason is simply that the RESTO site is much larger in area than DEGRD; the restoration project produced a channel nearly twice as wide as that at DEGRD at normal flows, with velocities 40–50% lower. A wider, slower channel no doubt provides more area where newly emerged fry can feed productively. However, higher availability of velocity shelter and hiding cover at RESTO no doubt contributed to higher retention, survival, and growth of juveniles. (We did not evaluate the potential for the wider, slower channel to result in higher temperatures.)

Differences between sites in total production of juvenile Chinook Salmon were small, in part because spawning gravel was also abundant at DEGRD (perhaps due to upstream gravel injection as part of the restoration program) and because most juveniles migrate downstream soon after emerging from the redd. The redd scour function in inSALMO indicates that the restored site is considerably less vulnerable to redd mortality due to high flows.

### General Conclusions for Habitat Restoration

One important general conclusion of this study is that restoration actions can have different, even opposing, effects on pro-

duction of small, newly emerged, juvenile salmon versus production of juveniles that survive and grow before migrating downstream. Our simulations indicated that widening and reshaping the channel and (from the limiting factors analysis) increasing the availability of food, velocity shelter, and hiding cover all had little effect on production of small out-migrants but strong positive effects on the number of large out-migrants. Increasing spawning gravel availability increased production of small out-migrants while having small and sometimes negative effects on the number of large ones. If evidence that large out-migrants are more important (e.g., Miller et al. 2010) is confirmed or accepted, it will be increasingly important for restoration project design to consider juvenile rearing habitat. Jeffres and Moyle (2012) recently expressed concern about designing habitat projects to enhance spawning success without giving adequate consideration to juvenile life stages.

A second general conclusion is that, in our simulation experiments, a variety of factors affected restoration benefits—especially the number of large out-migrants—in a generally multiplicative way, instead of there being a clear “limiting factor.” We did not find just one process or variable that limited out-migrant production, but instead several factors—food availability, velocity shelter, hiding cover—that each have strong effects. Such results are typical of our individual-based fish models that include behaviors trading off feeding and predation avoidance (e.g., Harvey and Railsback 2007; Railsback and Harvey 2011). This conclusion implies it is not always necessary, or even possible, to identify a “limiting factor” before implementing a successful habitat improvement project.

Finally, our limiting factors analysis supports the conclusion that total production of salmon may be improved the most if enhancement efforts are concentrated in areas of especially good habitat instead of dispersed among many unproductive areas. This analysis indicated that further enhancements, such as increasing food production or cover availability, would produce independent and multiplicative increases in production of large out-migrants. When multiple habitat factors have independent, multiplicative effects, the benefits of improving those factors are highest where juvenile production is already high. For example, an addition of hiding cover that reduces predation mortality by 10% will save more fish at a site producing 1,000 fish than at one producing 100 fish (assuming that there is not extreme competition for escape cover during predation events). Creation of “hot spots” with high habitat quality for juvenile feeding and predator avoidance as well as spawning may be an effective salmon restoration technique.

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## REFERENCES

- Beacham, T. D., and C. B. Murray. 1990. Temperature, egg size, and development of embryos and alevins of five species of Pacific salmon: a comparative analysis. *Transactions of the American Fisheries Society* 119:927–945.
- Beechie, T. J., D. A. Sear, J. D. Olden, G. R. Pess, J. M. Buffington, H. Moir, P. Roni, and M. M. Pollock. 2010. Process-based principles for restoring river ecosystems. *BioScience* 60:209–222.
- Bernhardt, E. S., and M. A. Palmer. 2011. River restoration: the fuzzy logic of repairing reaches to reverse catchment scale degradation. *Ecological Applications* 21:1926–1931.
- Bernhardt, E. S., M. A. Palmer, J. D. Allan, G. Alexander, K. Barnas, S. Brooks, J. Carr, S. Clayton, C. Dahm, J. Follstad-Shah, D. Galat, S. Gloss, P. Goodwin, D. Hart, B. Hassett, R. Jenkinson, S. Katz, G. M. Kondolf, P. S. Lake, R. Lave, J. L. Meyer, T. K. O'Donnell, L. Pagano, B. Powell, and E. Sudduth. 2005. Synthesizing U.S. river restoration efforts. *Science* 308:636–637.
- Booker, D. J., D. A. Sear, and A. J. Payne. 2001. Modelling three-dimensional flow structures and patterns of boundary shear stress in a natural pool–riffle sequence. *Earth Surface Processes and Landforms* 26:553–576.
- Bovee, K. D. 1982. A guide to stream habitat analysis using the instream flow incremental methodology. U.S. Fish and Wildlife Service FWS/OBS-82/26.
- Earley, J. T., D. J. Colby, and M. R. Brown. 2010. Juvenile salmonid monitoring in Clear Creek, California, from October 2008 through September 2009. U.S. Fish and Wildlife Service, Red Bluff Fish and Wildlife Office, Red Bluff, California. Available: [www.fws.gov/redbluff/cvpia.aspx](http://www.fws.gov/redbluff/cvpia.aspx). (June 2012).
- Gard, M. 2006. Modeling changes in salmon spawning and rearing habitat associated with river channel restoration. *International Journal of River Basin Management* 4:201–211.
- Giovannetti, S. L., M. R. Brown, and L. A. Stafford. 2008. Fall Chinook Salmon spawning area mapping for the Clear Creek restoration program, 2007. U.S. Fish and Wildlife Service, Red Bluff Fish and Wildlife Office, Red Bluff, California. Available: [www.fws.gov/redbluff/cvpia.aspx](http://www.fws.gov/redbluff/cvpia.aspx). (June 2012).
- Grimm, V., and S. F. Railsback. 2005. Individual-based modeling and ecology. Princeton University Press, Princeton, New Jersey.
- Harvey, B. C., and S. F. Railsback. 2007. Estimating multi-factor cumulative watershed effects on fish populations with an individual-based model. *Fisheries* 32:292–298.
- Harvey, B. C., and S. F. Railsback. 2009. Exploring the persistence of stream-dwelling trout populations under alternative real-world turbidity regimes with an individual-based model. *Transactions of the American Fisheries Society* 138:348–360.
- Haschenburger, J. K. 1999. A probability model of scour and fill depths in gravel-bed channels. *Water Resources Research* 35:2857–2869.
- Hayes, J. W., N. F. Hughes, and L. H. Kelly. 2007. Process-based modelling of invertebrate drift transport, net energy intake and reach carrying capacity for drift-feeding salmonids. *Ecological Modelling* 207:171–188.
- Healey, M. C. 1991. Life history of Chinook Salmon (*Oncorhynchus tshawytscha*). Pages 311–394 in C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.
- Healey, M. C., and W. R. Heard. 1984. Inter- and intra-population variation in the fecundity of Chinook Salmon (*Oncorhynchus tshawytscha*) and its relevance to life history theory. *Canadian Journal of Fisheries and Aquatic Sciences* 41:476–483.
- Honea, J. M., J. C. Jorgensen, M. M. McClure, T. D. Cooney, K. Engie, D. Holzer, and R. Hilborn. 2009. Evaluating habitat effects on population status: influence of habitat restoration on spring-run Chinook Salmon. *Freshwater Biology* 54:1576–1592.
- Jähnig, S. C., A. W. Lorenz, D. Hering, C. Antons, A. Sundermann, E. Jedicke, and P. Haase. 2011. River restoration success: a question of perception. *Ecological Applications* 21:2007–2015.
- Jeffres, C., and P. Moyle. 2012. When good fish make bad decisions: Coho Salmon in an ecological trap. *North American Journal of Fisheries Management* 32:87–92.
- Korman, J., S. J. D. Martell, and C. Walters. 2011. Describing population dynamics for early life stages of Rainbow Trout (*Oncorhynchus mykiss*) using a stock synthesis model. *Canadian Journal of Fisheries and Aquatic Sciences* 68:1110–1123.
- Mesa, M. G., and C. D. Magie. 2006. Evaluation of energy expenditure in adult spring Chinook Salmon migrating upstream in the Columbia River basin: an assessment based on sequential proximate analysis. *River Research and Applications* 22:1085–1095.
- Miller, J. A., A. Gray, and J. Merz. 2010. Quantifying the contribution of juvenile migratory phenotypes in a population of Chinook Salmon *Oncorhynchus tshawytscha*. *Marine Ecology Progress Series* 408:227–240.
- NSR (North State Resources), McBain and Trush, and Matthews and Associates. 2000. Lower Clear Creek floodway rehabilitation project: channel reconstruction, riparian vegetation, and wetland creation design document. Report to the Clear Creek Restoration Team, NSR, Redding, California, McBain and Trush, Arcata, California, and Matthews and Associates, Weaverville, California. Available: [www.srwp.org/documents/watershed/lowerclearcreek/restfish/LwrClearCreek\\_FloodwayRehabProject08-30-00.pdf](http://www.srwp.org/documents/watershed/lowerclearcreek/restfish/LwrClearCreek_FloodwayRehabProject08-30-00.pdf). (June 2012).
- Railsback, S. F., and B. C. Harvey. 2001. Individual-based model formulation for Cutthroat Trout, Little Jones Creek, California. U.S. Forest Service General Technical Report PSW-GTR-182.
- Railsback, S. F., and B. C. Harvey. 2002. Analysis of habitat-selection rules using an individual-based model. *Ecology* 83:1817–1830.
- Railsback, S. F., and B. C. Harvey. 2011. Importance of fish behaviour in modelling conservation problems: food limitation as an example. *Journal of Fish Biology* 79:1648–1662.
- Railsback, S. F., B. C. Harvey, S. K. Jackson, and R. H. Lamberson. 2009. InSTREAM: the individual-based stream trout research and environmental assessment model. U.S. Forest Service General Technical Report PSW-GTR-218.
- Railsback, S. F., B. C. Harvey, and J. L. White. 2012. InSALMO version 1.0: model improvements and demonstration application to Chinook Salmon spawning, incubation, and rearing in Clear Creek, California. Final Report to U.S. Bureau of Reclamation, Lang, Railsback and Associates, and U.S. Forest Service, Redwood Sciences Laboratory, Arcata, California. Available: [www.fws.gov/sacramento/Fisheries/Instream-Flow/fisheries\\_instream-flow\\_inSalmo.htm](http://www.fws.gov/sacramento/Fisheries/Instream-Flow/fisheries_instream-flow_inSalmo.htm). (June 2012).
- Railsback, S. F., R. H. Lamberson, B. C. Harvey, and W. E. Duffy. 1999. Movement rules for individual-based models of stream fish. *Ecological Modelling* 123:73–89.
- Railsback, S. F., H. B. Stauffer, and B. C. Harvey. 2003. What can habitat preference models tell us? tests using a virtual trout population. *Ecological Applications* 13:1580–1594.
- Roni, P., K. Hanson, and T. Beechie. 2008. Global review of the physical and biological effectiveness of stream habitat rehabilitation techniques. *North American Journal of Fisheries Management* 28:856–890.
- Steffler, P., and J. Blackburn. 2002. River2D—two-dimensional depth averaged model of river hydrodynamics and fish habitat: introduction to depth averaged modeling and user's manual. University of Alberta, Edmonton. Available: [www.river2d.ualberta.ca/download.htm](http://www.river2d.ualberta.ca/download.htm). (June 2012).
- Stewart-Koster, B., S. E. Bunn, S. J. MacKay, N. L. Poff, R. J. Naiman, and P. S. Lake. 2010. The use of Bayesian networks to guide investments in flow and catchment restoration for impaired river ecosystems. *Freshwater Biology* 55:243–260.
- USFWS (U.S. Fish and Wildlife Service). 2005. Monitoring of restoration projects in Clear Creek using 2-dimensional modeling methodology. USFWS, Sacramento Fish and Wildlife Office, Sacramento, California.

- USFWS (U.S. Fish and Wildlife Service). 2006. Phase 3A Clear Creek restoration: 2-d modeling. USFWS, Final Report, Sacramento Fish and Wildlife Office, Sacramento, California. Available: [www.fws.gov/sacramento/Fisheries/Instream-Flow/fisheries\\_instream-flow\\_reports.htm](http://www.fws.gov/sacramento/Fisheries/Instream-Flow/fisheries_instream-flow_reports.htm). (June 2012).
- Walters, C. J. 1986. Adaptive management of renewable resources. Macmillan, New York.
- Walters, C. J., and C. S. Holling. 1990. Large-scale management experiments and learning by doing. *Ecology* 71:2060–2068.
- Walters, C. J., J. Korman, L. E. Stevens, and B. Gold. 2000. Ecosystem modeling for evaluation of adaptive management policies in the Grand Canyon. *Conservation Ecology* [online serial] 4(2):article 1.
- Wheaton, J. M., G. B. Pasternack, and J. E. Merz. 2004. Spawning habitat rehabilitation: I. conceptual approach and methods. *International Journal of River Basin Management* 2:3–20.
- Yoshiyama, R. M., E. R. Gerstung, F. W. Fisher, and P. B. Moyle. 2000. Chinook Salmon in the California Central Valley: an assessment. *Fisheries* 25(2):6–20.