

# EFFECTS OF SPATIAL EXTENT ON SIMULATED RELATIONS BETWEEN HABITAT AND SALMON POPULATIONS

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## ABSTRACT

We address the question of spatial extent: to make results representative of the entire stream, how much space, of what kinds, needs to be represented in models of stream habitat effects on fish populations? Our analysis used inSALMO, an individual-based model of salmon spawning, incubation, and juvenile rearing. The model was applied to 12 sites, totaling 4.0 km length, on the lower 14 km of Clear Creek, California. Simulation experiments examined responses of salmon spawning and rearing success to habitat variables such as flow and temperature, when the model included each individual site, all sites, and random combinations of two to nine sites. Some responses, such as temperature effects on egg incubation, were insensitive to spatial extent. Other responses, including effects of flow on production of larger juveniles, varied sharply among sites. Most small sites had little effect on overall results, but one small site provided exceptionally good juvenile rearing habitat and strongly affected responses of the entire stream. Larger sites (length > 15 channel widths) in distinct habitat types (e.g., highly disturbed and recently restored) also had strong effects. Including more or longer sites generally increased model representativeness but not consistently. Results highly representative of the entire stream could also be obtained by combining large sites in typical habitat with “hot spots” of especially productive habitat. For salmon, being lower in the watershed may increase the effect of a site on results.

**KEY WORDS:** Chinook salmon; habitat; individual-based model; instream flow; sites; space; spawning success

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## INTRODUCTION

The issue of spatial extent is of general interest in ecological modeling: how do predicted effects of habitat on populations depend on how much habitat is represented in a model? This issue has been particularly of interest for river management and the models used to support decisions such as how much flow is needed to support fish populations. Questions such as how many study sites are needed, and how much space to represent at each site, have long been contentious in instream flow assessment (Gard, 2005; Kondolf *et al.*, 2000; Ladson *et al.*, 2006; Williams, 1996; Williams, 2010).

Several previous studies have developed relations between spatial extent and the precision or accuracy of instream flow model results (Gard, 2005; Williams, 2010). Those studies have, however, several limitations characteristic of current instream flow modeling practices (Railsback, 1999). Their focus is on how many transects are needed, but a transect—a slice across a channel, represented as series of point measurements—is one-dimensional and hence represents no space at all. More meaningful questions typically addressed in ecological modeling are: (1) how much space needs to be represented, (2) how should the represented areas be distributed within the stream, and (3) what should the spatial resolution (cell size) be (a question not addressed here). These questions can be addressed by explicitly assuming how much area each point on a transect represents, or by adopting the fully two-dimensional representation of stream area used in hydrodynamic models. A second limitation is that the habitat “suitability” approaches typically used do not produce results testable against independent field observations and do not consider the rapid changes in how habitat affects young fish as they grow.

Overcoming such limitations of habitat suitability models was a primary motivation for developing individual-based models (IBMs) for instream flow assessment (Van Winkle *et al.*, 1998). IBMs can link submodels for hydraulics, feeding and energetics, survival, and behavior to produce testable predictions of population response to river management factors such as flow and temperature regimes and channel shape (Railsback and Harvey, 2001; Railsback and Harvey, 2002; Railsback *et al.*, 2009; Railsback *et al.*, 2013).

However, the same issues of spatial extent are relevant to IBMs. How sensitive are population responses predicted by an IBM to the amount and type of habitat represented by the model? Here, we use a salmon IBM in which spatial resolution is carefully chosen, space is represented as one or more stream reaches made up of habitat cells, habitat effects on fish growth and survival change continually with the size and condition of individual fish, and results are testable and meaningful.

### *Objectives*

In this study we take advantage of the large number of sites to which a salmon IBM has been applied on a relatively small stream (12 sites totaling 4.0 km, on 14 km of stream). This system lets us look at how model results vary among sites and at how results for the whole stream depend on how much space, and which sites, are included in a model analysis.

We address two specific objectives. First is to quantify the variability among individual sites in model-predicted habitat productivity and how it responds to changes in management variables such as flow, temperature, and spawning gravel availability. Habitat productivity is

evaluated as “spawning success”: the number of salmon juveniles that migrate downstream alive per female spawner. (Our definition of spawning success therefore includes any rearing that occurs within the natal stream.) This result is reported separately for total juveniles and for those that establish and grow at least a small amount before migrating out of the stream. The second objective is to examine how the model-predicted response to changes in one key management variable—flow—depends on how many and which sites are included. This objective targets the study design question: how much stream area, in what kinds of places, should be modeled to predict fish population response to management alternatives with reasonable precision?

## METHODS

The general approach we use is simulation experiments with inSALMO, an IBM of the freshwater life stages of salmon: spawning, egg incubation, and juvenile rearing and outmigration (Railsback *et al.*, 2013). This model can represent individual sites or combinations of sites in a stream network; we look at how model results differ when different combinations of sites on the same stream are simulated.

### *Study sites*

Our simulations represent lower Clear Creek (LCC), from the Clear Creek Road bridge at river kilometer (RK) 14 downstream to the creek’s confluence with the Sacramento River, in Shasta County near Redding, California (Figure 1). LCC supports relatively strong runs of anadromous salmonids, especially a fall run of Chinook salmon (*Oncorhynchus tshawytscha*). Surveys conducted by the California Department of Fish and Game indicate that numbers of fall Chinook spawning in the upper 7 km of LCC ranged from 3000 to 16,000 in 1998 through 2009. This run is generally confined to LCC by a cascade and a weir sometimes placed at the upper end of our study reach.

Except during high runoff events, flow and temperature in LCC is dominated by releases from Whiskeytown Reservoir at RK 29. The LCC channel is confined by a canyon at its upper end, but downstream from approximately RK 7.5 it passes through alluvial gravel deposits heavily disturbed by historic gold and gravel mining. Restoration actions since 1995 have included increased instream flows, injection of spawning gravel at several locations, removal of a small dam at RK 10.4, and a channel restoration project near RK 6.4 that appears to have improved spawning and rearing conditions (Railsback *et al.*, 2013).

We developed model input representing 12 sites that total 29% of the total length of LCC (Table 1). Three of the sites were originally developed to evaluate stream restoration activities; one site is an unrestored control (USFWS, 2005). The other sites were originally developed for habitat suitability assessment as part of instream flow studies (e.g., USFWS, 2011). Five of the sites were selected to represent spawning habitat and four to represent juvenile rearing habitat. Additional considerations in selecting the sites for the instream flow studies included suitability for two-dimensional hydrodynamic modeling and accessibility. Methods for developing input and calibrating the model are described in the Supplementary Information.

## *Salmon model*

The inSALMO model and its calibration and application to Clear Creek fall Chinook salmon were described by Railsback *et al.* (2013; 2011), and predecessor models have been extensively described and tested (e.g., Railsback and Harvey, 2002; Railsback *et al.*, 2009; Railsback *et al.*, 1999). A summary description is in the Supplementary Information.

inSALMO is a daily time step model. Each study site is represented as a “reach” made up of two-dimensional habitat cells. Reaches have daily input for flow, temperature, and turbidity, and cells have variables for depth, velocity, and several kinds of cover. The main processes simulated are: (1) Adult arrival and spawning: adult salmon are added to the model and they create redds in selected cells. (2) Incubation: eggs develop at a temperature-driven rate until ready to emerge as juveniles. (3) Juvenile rearing and outmigration. Juveniles select the best cell within a small radius for feeding, a tradeoff between growth and predation risk. If no such cell provides acceptable growth and risk, the juvenile instead migrates downstream into the next reach. When juveniles migrate out of the downstream-most reach they are recorded as “outmigrants” and removed from the model.

The spatial extent modeled in inSALMO is expected to affect results in at least two ways. As in all spatial models, a primary effect of spatial extent is determining how well the model represents the natural range and distribution of physical habitat. The second expected effect results from juveniles migrating downstream from reach to reach, potentially feeding as they go: the number and arrangement of reaches could affect the number and size of outmigrants surviving to the downstream end. Including more reaches, or longer reaches, provides more opportunities for juveniles to grow—and also to be eaten—before they are recorded as migrating out of the simulated system.

## *Simulation experiment design*

We used three simulation experiments to address our two objectives. All used the same measures of spawning success to indicate the habitat’s productivity for Chinook salmon spawning. These measures are the total number of live outmigrants and the number of “large” outmigrants (> 5 cm fork length) per female spawner. The large outmigrant measure is included to evaluate juvenile rearing: the model’s newly emerged fry have lengths between 3.5 and 4.1 cm, so outmigrants with length > 5 cm were able to establish and grow for at least a few days. Because this study is focused on effects of space, not temporal variability, results are reported as the mean over the five simulated years.

To provide context for the simulation experiments, which simulate one or several sites, we also simulated the entire set of 12 sites together. Results of these “all-sites” simulations were treated as the “true” responses of the salmon population to management variables: other simulations that most closely match the all-sites simulation results were considered—for this modeling study—the most accurate models of the real population.

**Individual site simulations.** The first simulation experiment evaluated variability among sites in habitat productivity by simulating each individual site by itself, with juveniles considered outmigrants when they leave the reach they were spawned in. Because all the sites were initialized with the same spawner density, the spawning success results indicate the relative ability of each site to support successful spawning, incubation, and juvenile rearing, independent of site length.

Instead of just simulating historic conditions, we looked at how simulated spawning success responds to habitat variables that are often river management options. This experiment used inSALMO's "limiting factors tool" (LFT; Railsback *et al.*, 2011), which automatically generates and executes simulations evaluating sensitivity of model results to factors potentially affected by river management. We examined four factors. The flow analysis added a constant modifier to daily flow; in five simulations, this modifier had values ranging from -2.0 to + 4.0 m<sup>3</sup>/s in steps of 1.5 m<sup>3</sup>/s. Similarly, the temperature analysis varied water temperature during the November-May incubation and rearing period by a modifier ranging from -4.0 to +4.0°C in steps of 2°C. The other analyses varied the relative availability of spawning gravel and velocity shelter (both the number of cells providing these resources and the amount per cell) from half to 1.5 times the baseline values.

**Multiple site simulations.** The second experiment modeled multiple sites and examined the question of how many sites are needed to produce model results that adequately represent the "true" population responses to habitat change. The experiment varied the number of sites, and which sites, were included in simulations that let juveniles migrate downstream from one site to the next. Results were the number of large outmigrants leaving the downstream-most reach, per spawner. Because longer sites have more spawners, these results are automatically "weighted" to be more affected by longer sites, assuming they represent more of the stream. We simulated five unique combinations each of 2, 4, 6, and 9 sites. The sites in each such combination were drawn randomly, without replacement (Table 2), retaining their actual upstream-to-downstream order. To keep this second experiment tractable, we only analyzed simulated response of spawning success to base flow. We examined only large (> 5 cm fork length) outmigrants because total outmigrant production varied little with flow (Results, below).

**All-but-one-site simulations.** The third simulation experiment was designed to determine which sites, and which kinds of sites, have the most effect on simulated responses of the entire population and, hence, are most important to include in the model. This question was addressed by simply simulating the entire system 12 times, each time leaving out one of the sites. The effect on results of leaving a site out was used as a measure of how strongly the site affects simulated responses. The system response used in the experiment was the effect of base flow on production of large outmigrants.

## RESULTS

### *Variation among sites at baseline conditions*

The number of total outmigrants per spawner was generally consistent among sites, with all but one site having a median between 2800 and 3500 (top panel, Figure 2). The Tarzan Pool site had much lower spawning success than others. Spawning gravel is sparse at that site, resulting in high superimposition mortality (84% of eggs).

Two kinds of results explain this consistency. First, egg mortality was consistent among sites. The primary source of egg mortality was superimposition of new redds over old ones; superimposition mortality generally ranged 40-50% among sites. Superimposition rates are largely driven by availability of spawning gravel, which is relatively abundant throughout LCC. Disease and direct mortality related to temperatures below or above optimal, a minor cause of egg loss, was also consistent among sites because temperature regimes differ little among sites. Second, a very high percentage of newly emerged salmon fry migrated downstream immediately

(in reality as well as in the simulations; Railsback *et al.*, 2013). Comparison of the upper and lower panels of Figure 2 indicate that fewer than one juvenile in 100 stayed long enough to reach 5 cm length. Hence, few outmigrants were affected by any differences among sites in rearing habitat.

Production of large outmigrants was more variable among sites (lower panel, Figure 2). In fact, the site with anomalously low production of total outmigrants (Tarzan Pool) was one of two with highest production of large outmigrants. This site has relatively good rearing habitat, and reduced competition (due to lower egg survival) probably also contributed to growth and survival of the fry that did emerge.

The simulated numbers of large outmigrants were not consistently related to the site characteristics identified in Table 1. Many of the sites chosen to represent juvenile rearing habitat had medium and high production of large juveniles, but one of those sites (North State Riffle) had very low production of large outmigrants and one site with high production of large outmigrants (Lower Gorge) was intended to represent spawning habitat.

The baseline simulations including all sites (the rightmost box and whiskers in Figure 2) differ from the individual-site simulations because juveniles in them had to migrate through all downstream reaches before being counted as successful outmigrants. These simulations produced a number of total outmigrants that was 99% of the sum over the individual-site simulations, indicating that (in these simulations) mortality during outmigration was very minor. The number of large outmigrants was 111% of the sum over individual-site simulations, indicating that growth during downstream migration could have at least modest effects on this result. The two sites with highest production of large outmigrants were highly selected by juveniles in the all-sites simulation: the mean number of live juveniles per unit stream length at Tarzan Pool and Lower Gorge were 180% and 160% of the mean across sites.

### *Experiment 1: Responses of individual reaches to habitat variables*

**Base flow.** Total production of outmigrants showed little consistent response to base flow (Figure 3, upper left panel), with about 3000 outmigrants per spawner over all flows and at all but one site. The exception, Tarzan Pool, has spawning gravel only near the channel margins; small increases in flow produce more suitable spawning habitat but further increases appear to produce velocities too high for spawning. The lack of response in total outmigrant production at most sites is due in part to spawning gravel being relatively widespread so suitable spawning habitat is available over the range of flows. However, the lack of response is also because the vast majority of juvenile salmon migrate downstream very soon after emerging from their redds and hence are not affected by feeding habitat conditions.

Simulated production of large outmigrants was more sensitive to flow and more variable among sites (Figure 3, lower left panel). At the sites producing the most large outmigrants per spawner, this measure of spawning success decreased as much as 70% as flow increased. At sites where spawning success was low (North State Riffle, Restoration 3C, Shooting Gallery), it was steady or even increased as flow increased.

The response of large outmigrant production to flow was less consistent at the smallest sites than among the largest sites. Some of the smallest sites (ACID Glide, Tarzan Pool) were the sites most sensitive to flow, while others (North State Riffle, Side Channel) were among the least sensitive. In contrast, the largest sites (Restoration 3B, Restoration 3A, Lower Renshaw) produced spawning success closer to the “true” values produced by simulating all sites.

(However, Restoration 3B produced a different trend, with success increasing slightly at the highest flows.)

**Temperature.** The simulated variation in water temperature produced a strong, non-linear response in total outmigrant production that was consistent among sites (Figure 3, top right panel). This response is due to egg mortality: inSALMO assumes that egg mortality due to thermal stress and disease increase as temperatures depart from a range of optimal temperatures that happens to coincide with actual temperatures at the Clear Creek sites. With temperatures reduced to 4°C below actual, virtually all eggs that were not killed via superimposition were killed by low temperatures. With temperature increased by 4°C, 30% of such eggs were killed by high temperatures.

The response of large outmigrant production to temperature clearly reflected egg mortality but was more complex and variable among sites (Figure 3, lower right panel). Production of large outmigrants was lowest at the lowest and highest temperatures, but the temperature change producing highest spawning success varied among sites. Several processes could explain the different response of large outmigrants. First, temperatures during fry emergence (January–March; Figure S1) may be ideal for egg incubation but below optimal for juvenile growth. Second, it is typical in inSALMO simulations to see strong effects of competition on growth: when abundance is reduced by egg mortality there is less competition among juveniles for the best feeding locations, so the fraction of juveniles staying and growing to > 5 cm length can increase. In addition, temperature can interact with habitat conditions to drive energetics and growth (Harvey and Railsback, 2007; Railsback and Harvey, 2002), so the effects of temperature change could differ among sites with different hydraulic characteristics.

**Spawning gravel availability.** Variation in spawning gravel availability had little simulated effect on either total or large outmigrant production (Figure 4, left panels). The exception is the Tarzan Pool site, the only site where gravel was especially scarce. At Tarzan Pool, increasing gravel availability above observed levels (>100% relative availability) sharply decreased superimposition mortality of eggs and, hence, production of outmigrants.

**Velocity shelter availability.** Availability of velocity shelter for drift feeding had no consistent effect on total outmigrant success at any sites, but production of large outmigrants increased with velocity shelter at most sites (Figure 4, right panels). Results of this experiment paralleled those of the base flow experiment: the effect of velocity shelter availability was strongest at the sites producing most large outmigrants; small sites varied widely in response; and the largest sites each produced results closely following (in both trend and magnitude of large migrants per spawner) those of all sites combined.

### *Experiment 2: Responses of multiple sites to flow*

This experiment examined the response of simulated spawning success to base flow, using five combinations each of two, four, six, and nine sites. All combinations except two (2-sites A; 4-sites B) reproduced the general pattern of large outmigrants per spawner decreasing as flow increases, up to the fourth flow scenario (base flow increased by 2.5 m<sup>3</sup>/s) (Figure 5). The deviation from the “true” results generally decreased as more sites were included.

To quantify how well results from each combination of sites reproduce the “true” trend in response to base flow, we calculated the root mean square error (RMSE) from the “true” values, after removing the mean difference. For each site combination displayed in Figure 5, we subtracted the mean difference in spawning success (over all flow scenarios) between the series and the “true” all-sites results from each point. We then calculated the RMSE between those

points and the “true” results. These RMSE values were then plotted as a function of the total length of stream modeled (Figure 6, which also includes comparable results for each individual site from the first experiment). The RMSE values are relatively small, less than about 10% of the spawning success values reported in Figure 5 for combinations of 4 or more sites. They indicate no simple relation between length of stream simulated and simulation accuracy, except that the combinations including > 3000 m of stream (out of the 4000-m total) all had low error. However, some of the long combinations had large errors and some relatively short combinations had low error. The individual site most closely matching all-sites results (Upper Renshaw) was one of the shortest sites, chosen just to represent spawning habitat (Table 1).

The Tarzan Pool site may be important to how closely a site combination matched “true” spawning success. This site is small, yet it produces high numbers of large outmigrants per spawner (Figure 2) and is near the downstream end of LCC where almost all outmigrants move through it. Of the 6-site combinations, the one that included Tarzan Pool (E) had much lower RMSE than the others. Only one of the 9-site combinations (C) did not include Tarzan Pool and it was the only with RMSE above 0.7. On the other hand, the 2-site combination including Tarzan Pool (B), and the site by itself, were especially poor at representing the whole system.

### *Experiment 3: Effects of individual sites on population response to flow*

When we simulated response of large outmigrant production in the entire LCC system, leaving out one site at a time, there was considerable variation in the effect of individual sites. In Figure 7, the magnitude of the black square for each site indicates the site’s effect on mean spawning success in the base flow experiment (how much the site moves the “All sites” curve in the lower left panel of Figure 3 up or down). The extent of the “whiskers” for each site indicate how much it changes the shape of the response to base flow: sites with long whiskers affect spawning success more at some flows than at others, and hence affect the shape of the “All sites” curve in the lower left panel of Figure 3. Sites that affect the shape of the response to flow are especially important because management decisions are typically based on the shape of simulated responses (e.g., where the peak is, where the response changes direction) instead of on the response magnitude.

Sites with mean effects near zero and small ranges of effects had little influence on simulated response of the entire system to flow; these included ACID Glide, North State Riffle, Upper Isolation, Lower and Upper Renshaw, Side Channel Run/Pool, and Shooting Gallery (sites 1, 6, 7, 8, 9, 11, 12; Figure 7). Lower Gorge had a strong positive effect on simulated production of large outmigrants, confirming it as a “hot spot” for large outmigrant production; but its effect on the response shape was moderate. Restoration 3C and 3A had relatively strong negative mean effects but also only moderate effects on the response shape. Tarzan Pool and Restoration 3B also had strong positive effects on large outmigrant production and also strongly affected the response shape, indicating that they are especially important for predicting response of the entire system.

## DISCUSSION

How important is the amount of space represented in a stream fish model to results used to support river management decisions? The extraordinary extent of habitat data collected in

LCC, and the ability of inSALMO to relate habitat to important measures of population status, allowed us to examine this question to an usual level.

### *Study limitations*

Our study has several limitations (in addition to being entirely simulation-based) that restrict the generality of its results. First, we intentionally ignored temporal variation in model results to focus on spatial variation. We did note substantial variation in results among the five years we simulated, even though the upstream reservoir makes flow and temperature relatively stable. This variation was due to habitat-related processes (temperature-related egg mortality, uncontrolled high flows during fry emergence), and strong density dependence in juvenile survival and growth. Second, the abundance of suitable spawning habitat at our sites no doubt reduced the effects of spatial extent on spawning success. The one site lacking abundant spawning habitat, Tarzan Pool, responded to flow and gravel availability much differently than other sites.

### *Effects of spatial extent*

Some simulated salmon population responses were insensitive to spatial extent. Our primary example was total outmigrant production: changes in the total number of juveniles migrating downstream out of the simulated system per female spawner, in response to variables such as flow and temperature, were remarkably consistent across sites. This insensitivity was simply because (a) spawning gravel was abundant, and (b) the vast majority of such juveniles migrated downstream immediately after emergence and hence were little exposed to habitat conditions except those affecting spawning and egg incubation.

Many important model results, however, varied strongly among sites and were clearly affected by the model's spatial extent. Spawning success as the number per spawner of large outmigrants (fork length > 5 cm) varied widely among sites, as did its response to habitat variables such as flow and temperature. Increasing base flow, for example, produced fewer such outmigrants overall but the response at some sites was weak and even opposite the overall trend.

Given variation among sites in how they affect model results, are there kinds of sites that seem least important for predicting overall system response? Of the 12 sites we simulated, seven (ACID Glide, North State Riffle, Upper Isolation, Lower and Upper Renshaw, Side Channel Run/Pool, and Shooting Gallery) seemed to have little effect by themselves on the overall effects of base flow on production of large outmigrants. These are short sites, except Lower Renshaw. Lower Renshaw had little effect on overall response because its response to base flow was very similar to that of all the sites together (Figure 3).

What kinds of sites seemed most important to results? Our third experiment identified two sites, Restoration 3B and Tarzan Pool, as having strongest effects on the shape of the simulated response of spawning success to base flow. These two sites are quite different: Tarzan Pool is among the shortest sites while Restoration 3B is by far the longest. In our first experiment, production of large outmigrants decreased very sharply with increasing flow at Tarzan Pool, whereas the response at Restoration 3B was similar to that of the whole system except at the higher flows (Figure 3). Another site, Restoration 3C, was also among those with most effects on results but apparently for a third reason: production of large outmigrants was unusually poor at all flows. These three sites do have one common characteristic: they are near the downstream end of LCC, so almost all juveniles migrating downstream pass through them.

The individual sites producing results (Figure 3-Figure 4) most similar to results for all sites were Restoration 3B, Upper Renshaw, and Upper Isolation. This observation is not surprising for Restoration 3B because of its great length, but we had no indication *a priori* that Upper Renshaw and Upper Isolation—both relatively short and intended to represent spawning, not rearing, habitat—would be especially representative of the entire LCC.

### *Conclusions for modeling habitat effects on fish*

Despite its limitations, our study supports several conclusions of general value. First, it confirms the conclusion of Jeffres and Moyle (2012) and Railsback *et al.* (2013) that modeling and management for one life stage—spawning—can produce results that are misleading or even counterproductive for later life stages such as large outmigrants. If we had analyzed inSALMO results only for production of total outmigrants, we would have concluded that spatial variation and model extent was relatively unimportant. However, production of outmigrants that grew after emergence differed quite sharply among sites.

A second general conclusion is that a few processes through which habitat affects stream fish are not very variable over space. The example in this study was temperature effects on egg incubation: temperature varies only gradually over stream length and its effects on eggs do not interact strongly with other variables in our model. (They may, however, interact with variables such as in-gravel dissolved oxygen that we did not model.) For such processes, spatial extent should be unimportant; modeling small areas at large spatial intervals should suffice.

Because the 12 study sites responded to some variables, especially base flow, in different ways, modeling stream fish population responses to habitat using only a few or very small sites (e.g., 3-4 sites representing only a few channel widths each) appears unlikely to produce results accurately representing an entire stream. While we found that at least some combinations of only 2-4 sites represented general trends fairly well, many other combinations did not. And our sites were relatively large: only one was less than four channel widths in length.

Another conclusion relevant to instream flow study design is that the *a priori* judgments of which sites represented good juvenile rearing habitat (Table 1) were not consistently supported by simulation results. The lack of consistent correspondence could result from model error, but suggests that such judgments can be a source of error if study design is overly dependent on them.

Similarly, predicting which sites are especially representative of an entire stream appears risky. Several sites represented all of LCC well, but there was reason *a priori* to expect only one of them to do so: Restoration 3B, because it is by far the longest site. (Restoration 3B is also a channel restoration site, perhaps suggesting instead that it should be especially unrepresentative.) There was little reason to expect the other sites that produced results especially representative of the entire stream to do so.

“Hot spot” sites can be important to represent but should not be treated as indicative of how a whole stream responds. The Tarzan Pool site was a “hot spot” of habitat for juvenile rearing, strongly affecting predicted production of large outmigrants from the entire LCC. However, results for Tarzan Pool by itself were very different from those of other sites, and unrepresentative of the entire stream. Especially productive rearing habitat may be more important to represent if it is lower in the watershed and hence available to more juveniles as they move downstream.

Overall, our results point to two strategies for achieving model results representing a stream reasonably well; both strategies resemble long-advocated approaches. One is selecting

sites randomly, as in our second simulation experiment, using sufficient numbers of sites to make it likely that results are representative (Williams, 2010). Our experiment indicates that this strategy requires a relatively large spatial extent to make high representativeness likely. The second strategy is to combine small areas of especially productive habitat (“hot spots”) with larger areas each chosen to represent a more widespread habitat type (e.g., degraded and restored alluvial habitat represented by Restoration 3C and 3B, and canyon habitat represented by Upper Renshaw). A key limitation of this approach is the need to identify hot spots before modeling starts.

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## TABLES

Table 1. Site (model reach) characteristics. Total simulated length is 4000 m.

Name	RK	Length (m)	Mean width (m)	Description
1: ACID Glide	2.6	120	23	Juvenile rearing site
2: Tarzan Pool	3.0	158	24	Juvenile rearing site
3: Restoration 3C	4.3	455	17	Unrestored control site; steep and confined
4: Restoration 3B	5.0	1230	26	Channel restoration site; juvenile rearing site
5: Restoration 3A (2008)	6.4	519	29	Channel restoration site
6: North State Riffle	7.5	64	28	Juvenile rearing site
7: Upper Isolation	8.1	206	33	Spawning site
8: Lower Renshaw	8.6	479	35	Spawning site
9: Upper Renshaw	9.0	118	28	Spawning site
10: Lower Gorge	10.1	296	19	Spawning site
11: Side Channel Run/Pool	11.4	139	32	Juvenile rearing site
12: Shooting Gallery	12.1	215	25	Spawning site

Table 2. Random site combinations.

Combination	Sites included (site numbers from Table 1)	Stream length simulated (m)
2Sites-A	6, 12	279 (7% of total)
2S-B	2, 3	613 (15%)
2S-C	8, 12	694 (17%)
2S-D	1, 5	639 (16%)
2S-E	10, 11	435 (11%)
4S-A	1, 7, 10, 11	761 (19%)
4S-B	6, 7, 8, 9	867 (22%)
4S-C	1, 3, 9, 11	833 (21%)
4S-D*	3, 4, 5, 11	2343 (59%)
4S-E	4, 5, 7, 10	2251 (56%)
6S-A	1, 4, 9, 10, 11, 12	2119 (53%)
6S-B	3, 6, 7, 8, 9, 10	1618 (40%)
6S-C	3, 4, 7, 10, 11, 12	2541 (64%)
6S-D	3, 4, 6, 7, 8, 12	2649 (66%)
6S-E	2, 3, 4, 5, 7, 10	2864 (72%)
9S-A	1, 2, 4, 5, 6, 7, 8, 10, 11	3211 (80%)
9S-B	2, 3, 4, 5, 6, 7, 8, 9, 12	3445 (86%)
9S-C	1, 4, 5, 6, 7, 9, 10, 11, 12	2908 (73%)
9S-D	2, 3, 4, 5, 6, 8, 9, 10, 12	3534 (88%)
9S-E	1, 2, 3, 4, 6, 7, 9, 10, 12	2863 (72%)

## FIGURE CAPTIONS

Figure 1. Lower Clear Creek, flowing from west to east through the 12 study sites.

Figure 2. Numbers of total (upper panel) and large (fork length > 5 cm; lower panel) outmigrants, from simulations of each site by itself. Sites are identified by their number in Table 1; values labeled “All” are from simulations including all sites. Plots represent the distribution of results from five simulated years; hence, each element of the box-and-whisker plot (lower whisker, lower end of box, median, etc.) indicates results for one year.

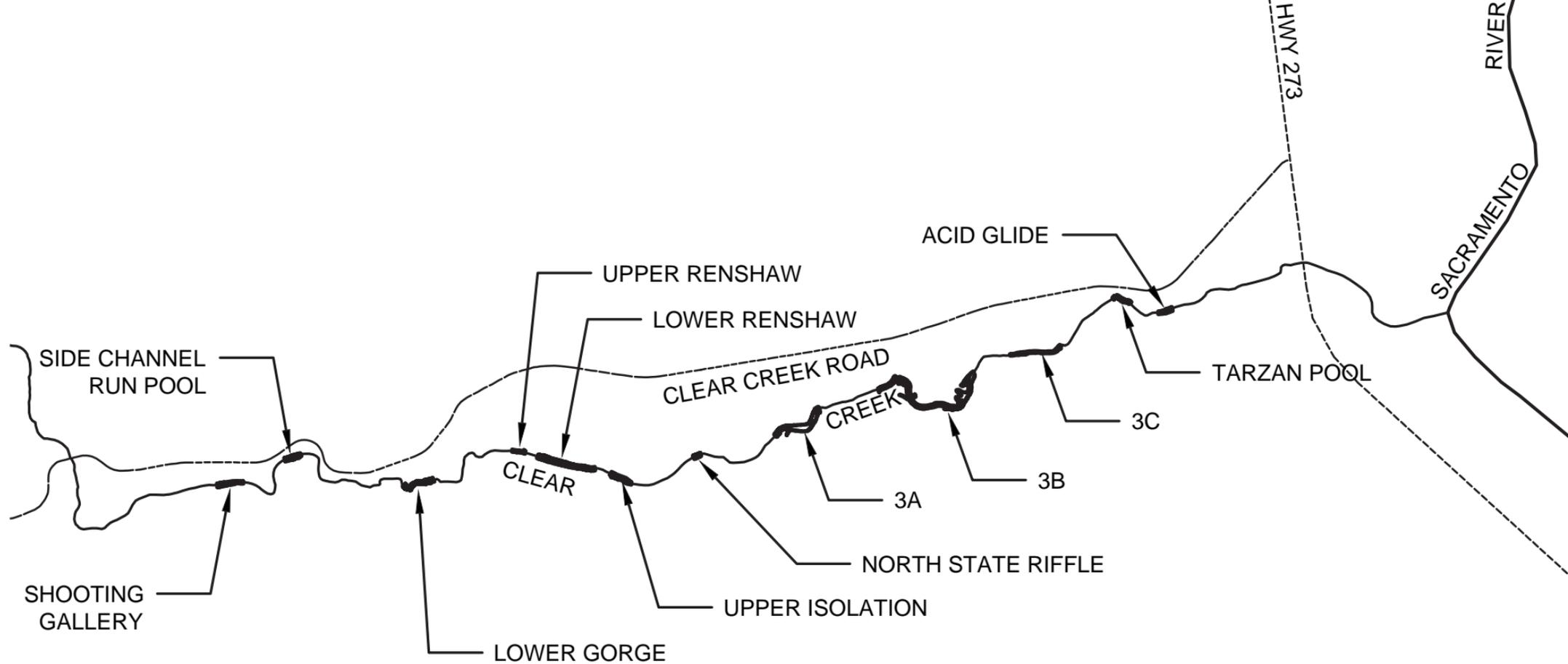
Figure 3. Simulated response of spawning success to base flow (left) and temperature (right), at each individual site. Top panels: total number of outmigrants per spawner. Lower panels: number of outmigrants with fork length > 5 cm per spawner. Results are the mean over five simulated years under each flow or temperature scenario.

Figure 4. Simulated response of spawning success to spawning gravel (left) and velocity shelter (right) availability; format as in Figure 3.

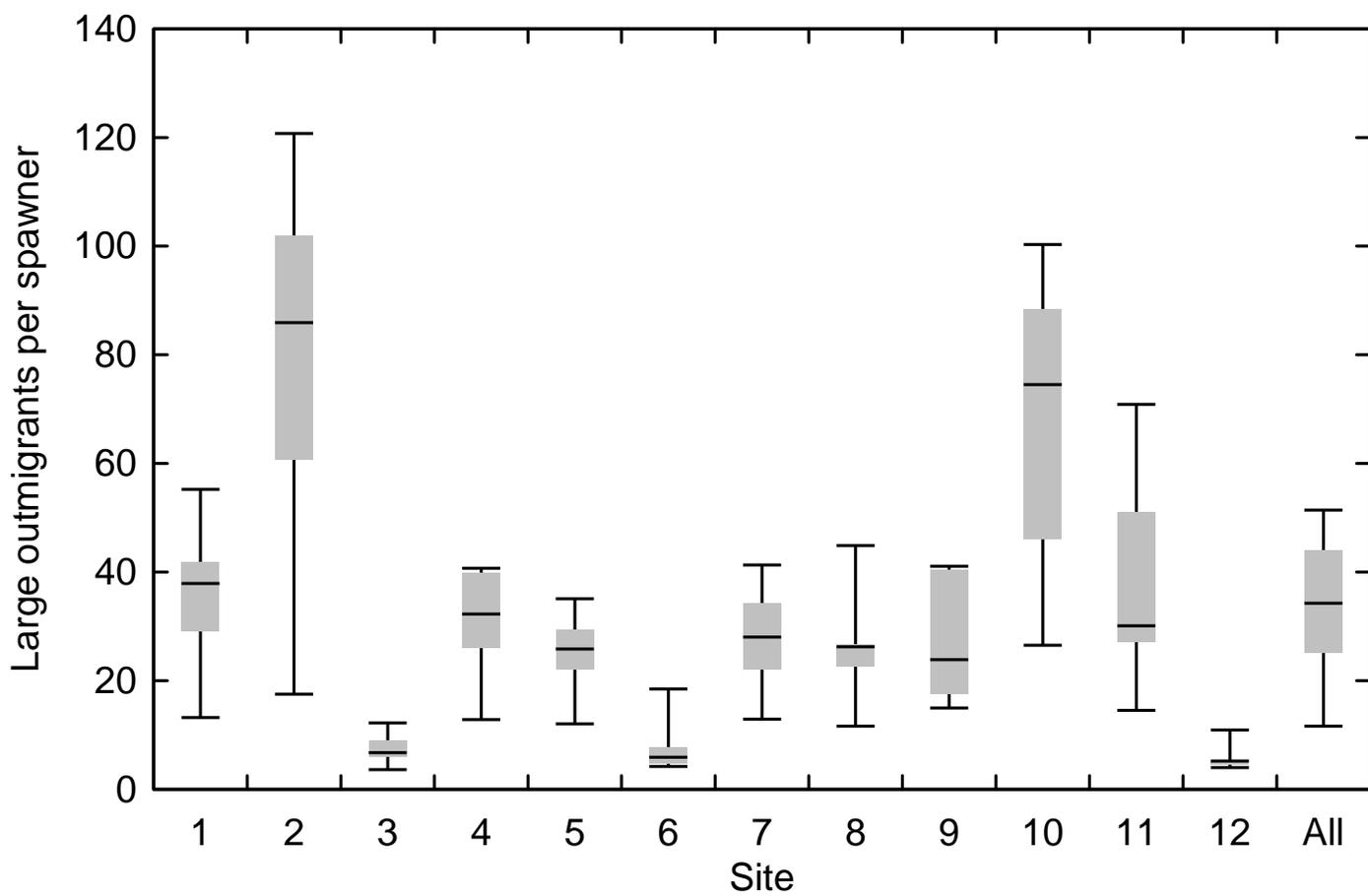
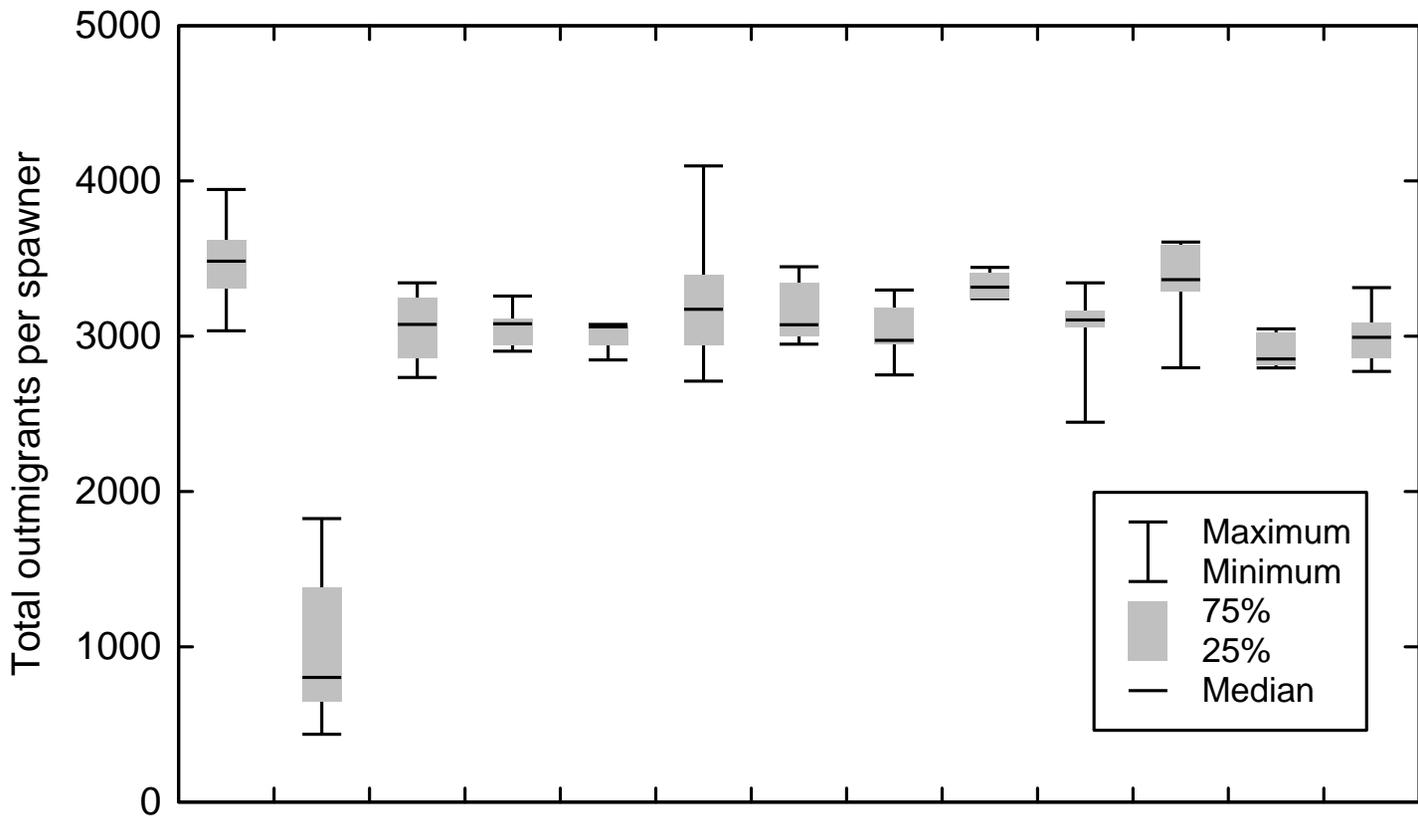
Figure 5. Multiple site experiment results: response of spawning success to base flow. Results are mean number of large outmigrants per spawner over five simulated years. Each panel displays results of five site combinations, defined in Table 2. For reference, each graph also displays the “true” results obtained from simulating all 12 sites together.

Figure 6. Root mean square error (RMSE) in simulated response to changes in base flow, after removing the mean difference between site combinations and the “true” all-site values. Each point represents one of the site combinations in Table 2 and Figure 5, or one of the individual sites (Figure 3, lower panel). The Y axis is the root mean square error in number of large outmigrants per spawner across the five flow scenarios, indicating the difference in trend of response to flow from “true” values. The X axis is the total length of stream simulated, from Table 2. One individual site (Tarzan Pool) is not displayed as it had an RMSE of 20.3 outmigrants per spawner.

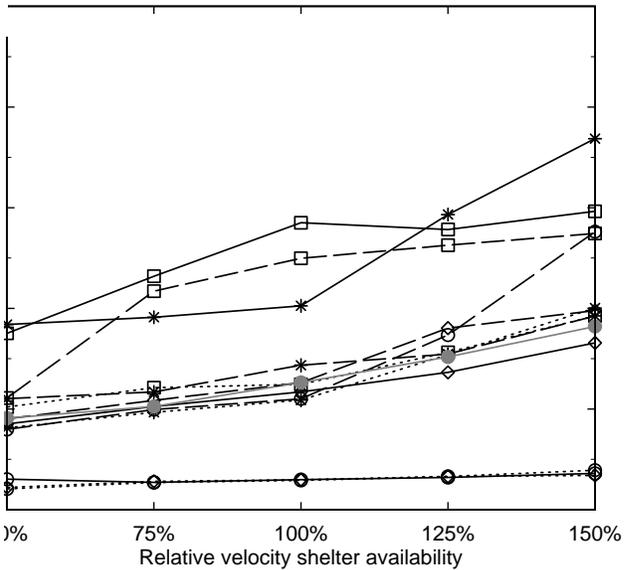
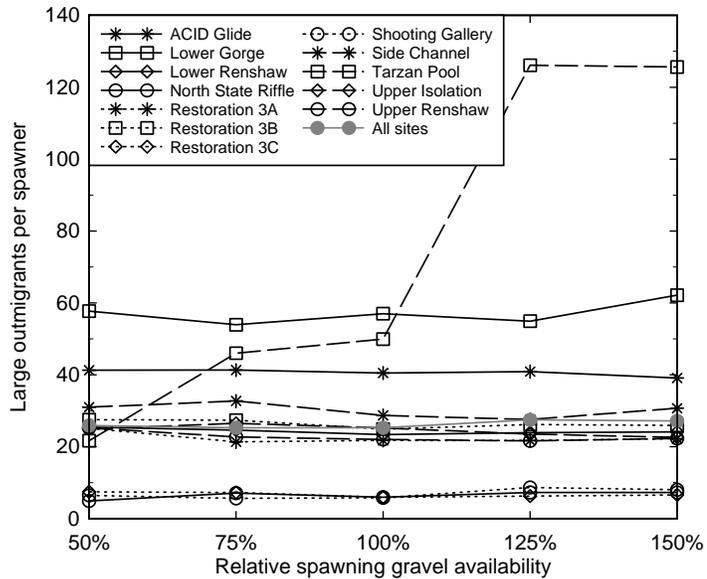
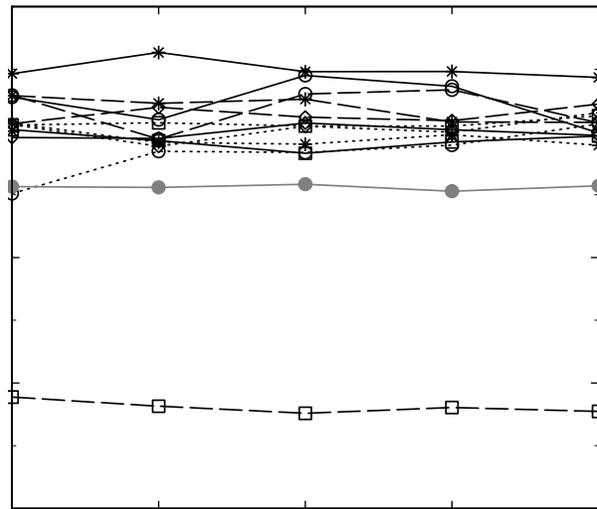
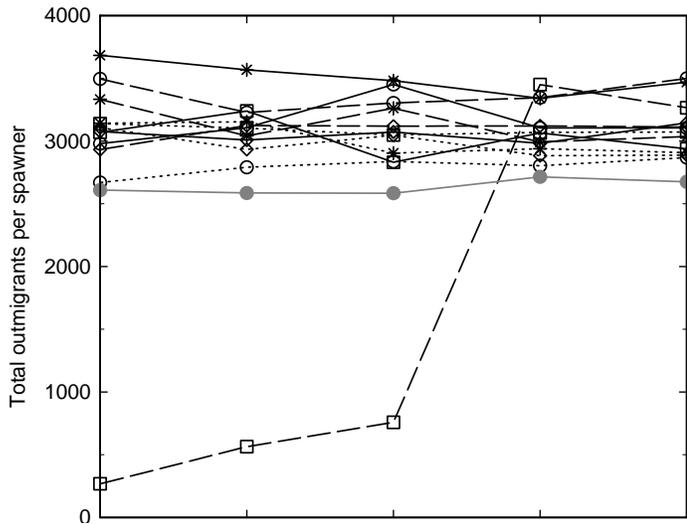
Figure 7. Effect of individual sites on simulated response of LCC spawning success (as mean number of large outmigrants per spawner, over five simulated years) to base flow. The Y axis represents the effect of individual sites (indicated on the X axis) on simulations of the entire LCC system: the difference in spawning success between simulations including all 12 sites and simulations excluding the site indicated by the X axis. The black squares represent the mean difference, and the “whiskers” represent the minimum and maximum difference, over five flow scenarios (as in Figure 3). Sites are identified by their number in Table 1.

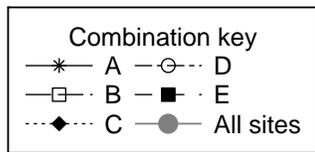
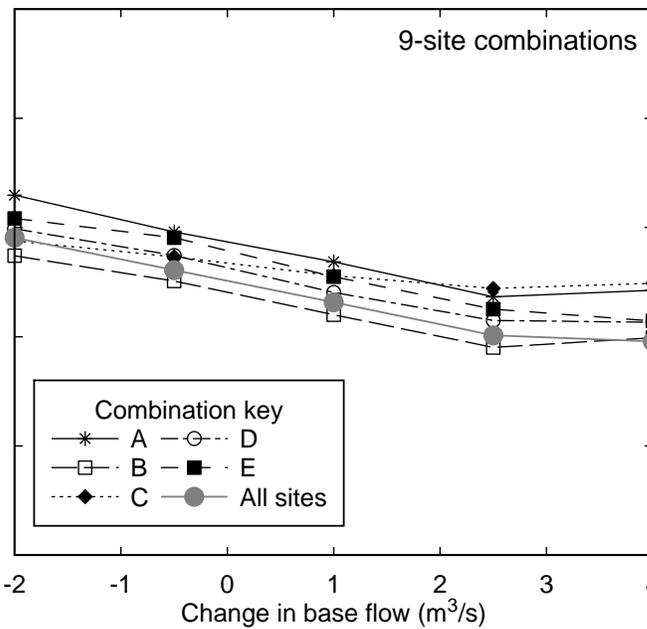
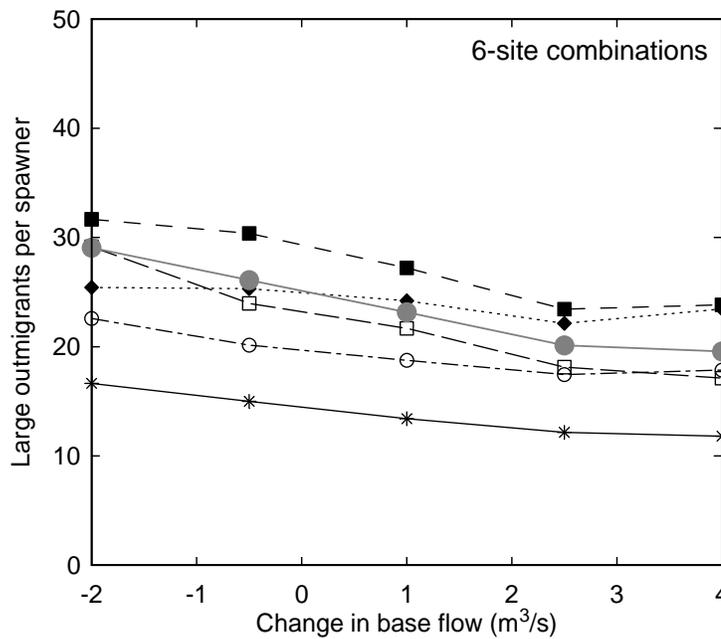
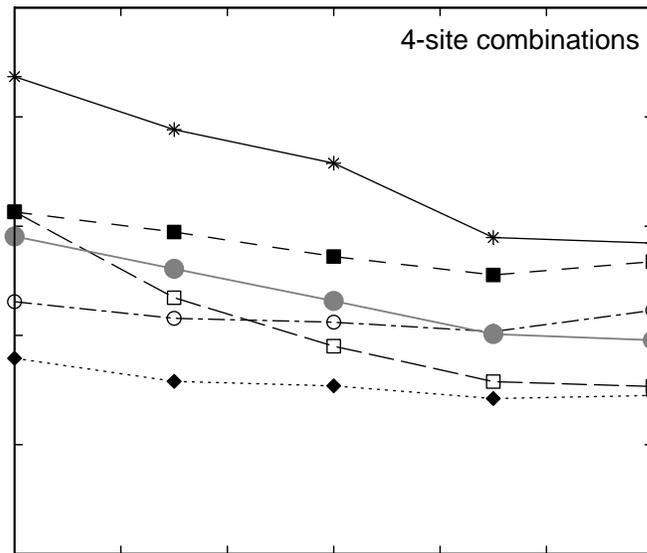
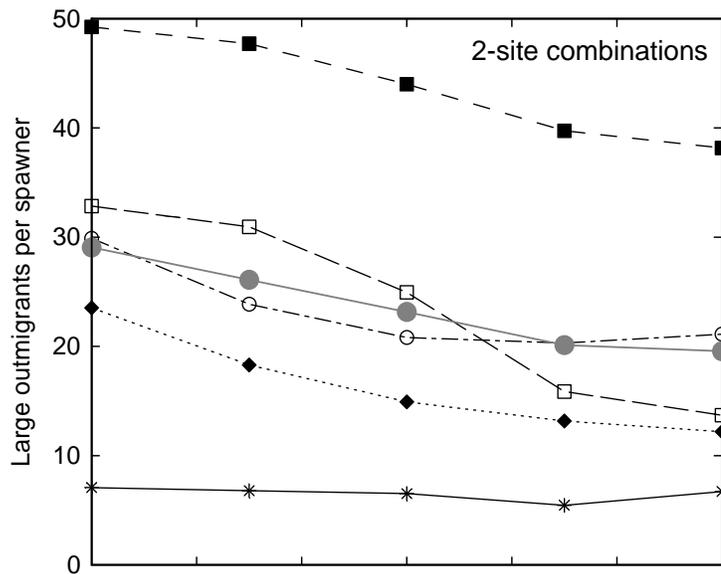


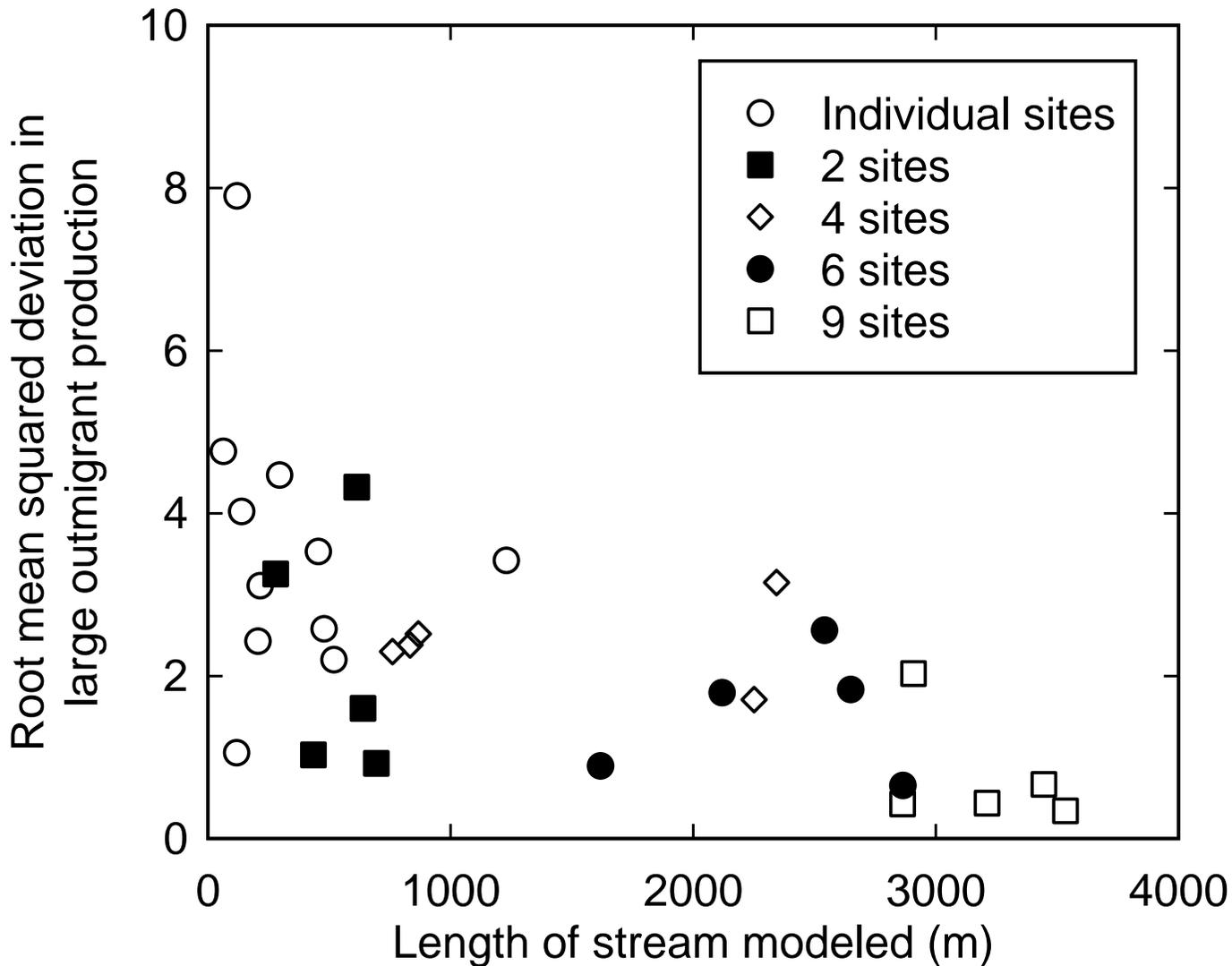
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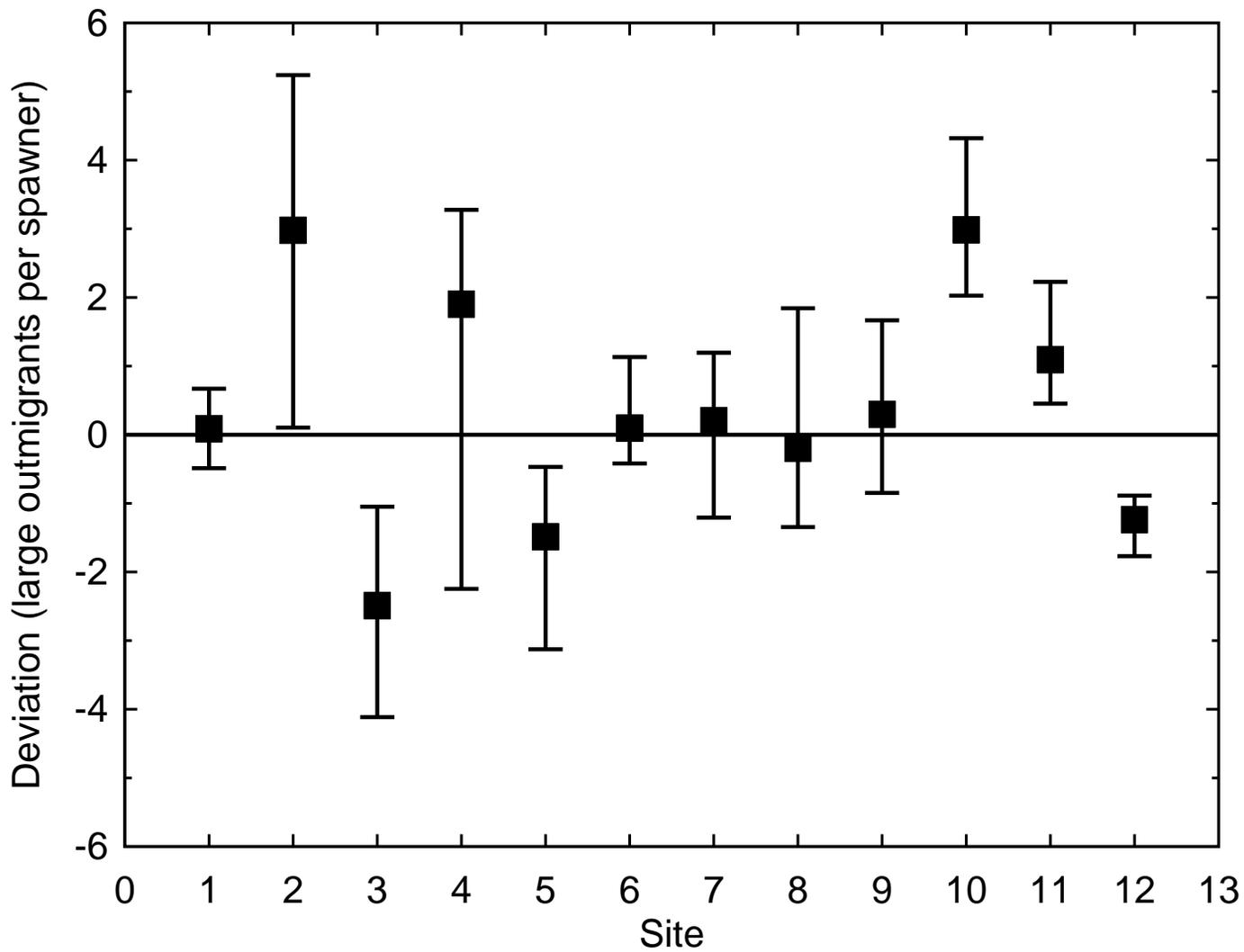












# EFFECTS OF SPATIAL EXTENT ON SIMULATED RELATIONS BETWEEN HABITAT AND SALMON POPULATIONS

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## SUPPLEMENTARY INFORMATION

### *Model summary*

**Model scales.** inSALMO operates at a daily time step. Habitat is depicted at two scales: reaches and cells. A reach represents a length of stream, typically several 100s of m in length; each simulation includes one or more reaches. (Each site in Table 1 is modeled as a reach.) Flow, temperature, and turbidity are daily inputs that can differ among reaches but are uniform within a reach. Each reach is made up of many cells, irregular polygons that each have their own depth, velocity, food availability, and availability of cover for drift-feeding and predator avoidance. The spatial resolution (minimum cell size, approximately 1 m<sup>2</sup>) was chosen as approximately the area used by one fish (super)individual to feed under typical drift-feeding conditions.

To make model execution speed reasonable, juvenile salmon are represented as “superindividuals”: each individual in the model represents 20 fish. This superindividual size has negligible effects on results (Railsback *et al.*, 2011).

**Adult arrival and spawning habitat selection.** Input for each reach defines the number, size and sex distribution, and arrival date ranges of adults arriving to spawn. Female adults spawn within a few days of arrival unless flows are unusually high or variable; all females spawn by the end of the spawning period (here, the months of October and November).

Upon spawning, females place a redd in the cell of their reach that has highest suitability, a function of depth, velocity, and area of unguarded spawning gravel. After spawning, females guard their redd against superimposition (other redds created in the same cell) for the few days that they survive.

**Incubation.** Redds develop at a temperature-dependent rate and their eggs are vulnerable to mortality due to superimposition, extreme temperature and disease, and desiccation if the cell is dewatered. When the development period is complete, surviving eggs are turned into new superindividuals representing juvenile salmon.

**Juvenile rearing and outmigration.** On each simulated day, juveniles select a habitat cell to feed in or decide to migrate downstream, feed and gain or lose weight, and undergo mortality risks. The habitat cell for feeding is selected from among a radius of nearby cells that increases with fish size but always includes the adjacent cells. Juveniles select the nearby cell offering the best expected future survival and growth (a function of their current size and condition, and the growth rate and mortality risk at a cell; Railsback *et al.*, 1999). Growth is

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modeled using feeding and bioenergetic methods that result in positive growth over a range of moderate velocities; this range widens and increases as a fish grows. Normally, juveniles select the cell offering lowest risk from those with positive growth; however, very young fish without access to moderate velocities (<~50 cm/s) experience negative growth and high risk of mortality due to energy depletion.

Juveniles decide to migrate downstream if expected future survival and growth in cells available in their current reach is less than a function that increases logistically with length (Railsback *et al.*, 2013). Hence, very young juveniles migrate downstream only if conditions in their reach make survival and growth very unlikely; but juveniles migrate more readily as they grow. When juveniles decide to migrate downstream, they are placed in the next downstream model reach; when they migrate out of the downstream-most reach they are recorded as “outmigrants” and removed from the model. Hence, outmigrant results from the model refer to juveniles that have moved downstream through all simulated reaches below their natal reach.

For juveniles able to obtain positive growth, the major causes of mortality are two kinds of predation. Risk of predation by fish is assumed high except in cells with low depths or abundant hiding cover, and decreases as juvenile length increases. Risk of predation by terrestrial animals (especially birds) is assumed high in shallow cells that lack cover, but very small fish are less vulnerable because they are less visible and less attractive as food.

**Processes not modeled.** Several processes that sometimes can be important to salmon spawning success were intentionally left out of inSALMO to avoid additional complexity. These include: (1) Male fertilization: eggs are assumed fertilized whether or not any adult males are present. (2) Gravel quality and sedimentation; no effects of spawning gravel quality or fine sediment deposition on egg survival are represented. Due in part to gravel augmentation, LCC gravel is generally clean and high-quality. (3) Redd scour: inSALMO can represent egg mortality due to scouring, but this function was disabled for this study because data to calibrate scour were lacking for many sites and because no extreme flows were simulated (discussed below at *Development of model input*). (4) Uncontrolled downstream movement of fry: newly emerged fry may be washed downstream in velocities exceeding their swimming ability, but inSALMO assumes fish can always maintain their position and move downstream only when they choose to. However, the model’s habitat selection and outmigration methods still result in many fry moving rapidly downstream because velocities exceeding their swimming ability produce rapid weight loss and high mortality risk. (5) Post-juvenile life stages and population dynamics: our simulations do not represent juveniles after they migrate out of Clear Creek, nor feedbacks of spawning success on adult abundance in subsequent years. Hence, results for one year are independent of results from previous years.

### *Development of model input*

We developed inSALMO model input for each of the 12 study sites, primarily from two kinds of information generated by previous habitat assessment studies (USFWS, 2005, 2011): calibrated two-dimensional hydraulic models, and detailed observations of substrate type and size and hiding cover type and size. The substrate and cover data, and bed topography observations used to define the hydraulic models’ finite element meshes, were obtained at high resolution, with site averages of 20 to 80 observations per 100 m<sup>2</sup> of stream (USFWS, 2011).

The first step in model input development was delineating habitat cells. We did this by manually selecting cell polygon vertices using a geographic information system (GIS). Cell delineation started with GIS layers showing depth contours at a typical base flow, plus the

substrate and cover observations. Cells were designed so each contains relatively similar habitat and borders between cells capture sharp changes in habitat, while making cells no smaller than necessary and not smaller than the  $\sim 1 \text{ m}^2$  minimum resolution.

The second step was developing a lookup table of cell average depth and velocity as a function of reach flow. The site's hydraulic model was run at 23 flows spanning the range of potential base flows ( $1.4$  to  $25 \text{ m}^3/\text{s}$ ). Because inSALMO simulates each day, the lookup tables must also include depths and velocities for the high flows that occasionally occur. Therefore, the hydraulic models were used outside their calibration range to predict depths and velocities at four additional flows ranging up to  $1400 \text{ m}^3/\text{s}$ . For each of these flows, depth and velocity were output from the hydraulic model on a square mesh with points spaced at  $0.6 \text{ m}$ . The depth and velocity of each inSALMO cell was calculated as the simple average (not weighted by area) of values from the square mesh points falling within the cell.

The third step was developing values for each cell's habitat variables: fraction of cell area with spawning gravel, fraction of area providing velocity shelter for drift feeding, and a characteristic distance to hiding cover. We developed an automated process to evaluate these variables in GIS from the substrate and cover observations and hydraulic simulations. First, Thiessen polygons were drawn around all the points where these observations were made, to define the area represented by each observation. The fraction of an inSALMO cell providing spawning gravel was then calculated as the fraction of cell area that was inside a Thiessen polygon for a field observation where substrate type is gravel suitable for Chinook spawning (diameter  $1.5\text{-}8 \text{ cm}$ ). Velocity shelter was assumed to be captured by the velocity gradients among nodes in the mesh used for hydraulic modeling. The fraction of an inSALMO cell providing velocity shelter was calculated as the fraction within a Thiessen polygon that was adjacent to another Thiessen polygon that (a) had velocity at least  $40\%$  lower, (b) had depth  $> 10 \text{ cm}$  (assuming fish would not feed in extremely shallow habitat), and (c) had not already been treated as shelter for a different polygon (the same low-velocity area is not treated as velocity shelter more than once, which would exaggerate its value as feeding habitat). Cells with velocity less than  $15 \text{ cm/s}$  are assumed to have no velocity shelter because shelter is not useful at such low velocities. Velocity shelter was calculated using velocities simulated at a stream flow of  $5.7 \text{ m}^3/\text{s}$ , for cells submerged at that flow (this is a common base flow during juvenile rearing); for cells only submerged at high flows, velocity shelter was calculated at  $25.5 \text{ m}^3/\text{s}$ . The characteristic distance to hiding cover of a cell was calculated by identifying 100 random points within the cell, calculating the distance between each of these points and the nearest field observation point where hiding cover (wood, branches, logs, overhead cover, undercut banks, aquatic vegetation, or large rocks) was present, and averaging the 100 distances.

Finally, we developed daily values of the flow, temperature, and turbidity input that drive inSALMO's habitat dynamics, for water years 2005-2009 (October 2004 through September 2009). Daily mean flows from the U.S. Geological Survey gage on Clear Creek near Igo (USGS 11372000), upstream of our sites at RK 18, was used as flow input for all sites. (There are no significant tributaries in LCC.) Temperature input for each site was obtained from the nearest of six temperature monitoring stations operated by the U.S. Fish and Wildlife Service's Red Bluff Fish and Wildlife Office. Turbidity input was developed from data collected approximately at the middle of the study area, near RK 7. Turbidity data were collected during water years 2003-2007, allowing computation of daily mean turbidity for 534 days. Using linear regression, flow at the Igo gage predicted turbidity for these days with  $R^2 = 0.76$ . We used this relationship to estimate turbidity for periods lacking direct measurements.

Flow, temperature, and turbidity are generally benign during the simulated period, largely due to the upstream reservoir. Monthly mean flows range from 2.8 (August) to 9.7 m<sup>3</sup>/s (March), and flow is never less than 2.0 m<sup>3</sup>/s (Figure S1). The period includes only 19 days with flow above the approximate channel-filling value of 25 m<sup>3</sup>/s, and the highest flow is 70 m<sup>3</sup>/s. Over all days and inputs, temperature (Figure S1) is always between 5.3 and 21.7°C, with a mean of 12.1°. Only 0.6% of values are above 20° (all occurring at gages downstream of that used for Figure S1). Monthly mean turbidities are < 5 NTU for all months, and only 13 days have turbidity > 20 NTU.

Characteristics of the spawner population were input for each simulated year and reach. For all sites and years, adult spawners were assumed to arrive at the sites during 2-30<sup>th</sup> October, with lengths drawn from a normal distribution with mean of 85 cm and standard deviation of 8.1 cm (lengths less than half the mean were re-drawn). The number of adults arriving at each reach was calculated by (1) keeping spawner density (number per km stream length) constant across sites and (2) representing the interannual variation in spawner density and sex ratio observed via redd and carcass counts conducted by the California Department of Fish and Game (Table S1). The simulated period includes years of low and high spawner density while having a mean equal to that of the 1998-2010 period of record (1200 spawners/km). Our methods for specifying spawner abundance mean that model results do not reflect differences among sites in spawner density, nor any feedback from spawning success one year on number of spawners in later years.

### *Calibration*

Railsback *et al.* (2013) calibrated inSALMO as applied to two of the LCC reaches (Restoration 3A and 3C). They adjusted parameters representing food availability, risk of predation by fish and terrestrial animals, and the function relating outmigration to juvenile length. Calibration objectives were to match several patterns observed in data from an outmigrant trap operated by the U.S. Fish and Wildlife Service near the downstream-most site. These patterns were in the (1) number of outmigrants with length > 5 cm, (2) date of last outmigration, (3) date on which mean outmigrant length exceeds 5 cm, and (4) maximum outmigrant length. Railsback *et al.* (2013) also showed that inSALMO generally reproduced observed redd locations.

For this study we tested how well the calibrated parameter values of Railsback *et al.* (2013) reproduced the same patterns when simulating all 12 sites together. This test led to one change: the value of the parameter *fishOutmigrantSuccessL1* was changed from 5 to 7 cm, making small juveniles tolerate lower fitness conditions in the stream before migrating downstream.

Table S1. Annual spawning population characteristics.

Year	Spawner density (per km)	Percent female
2005	2120	65%
2006	1210	57%
2007	590	64%
2008	1100	65%
2009	460	57%

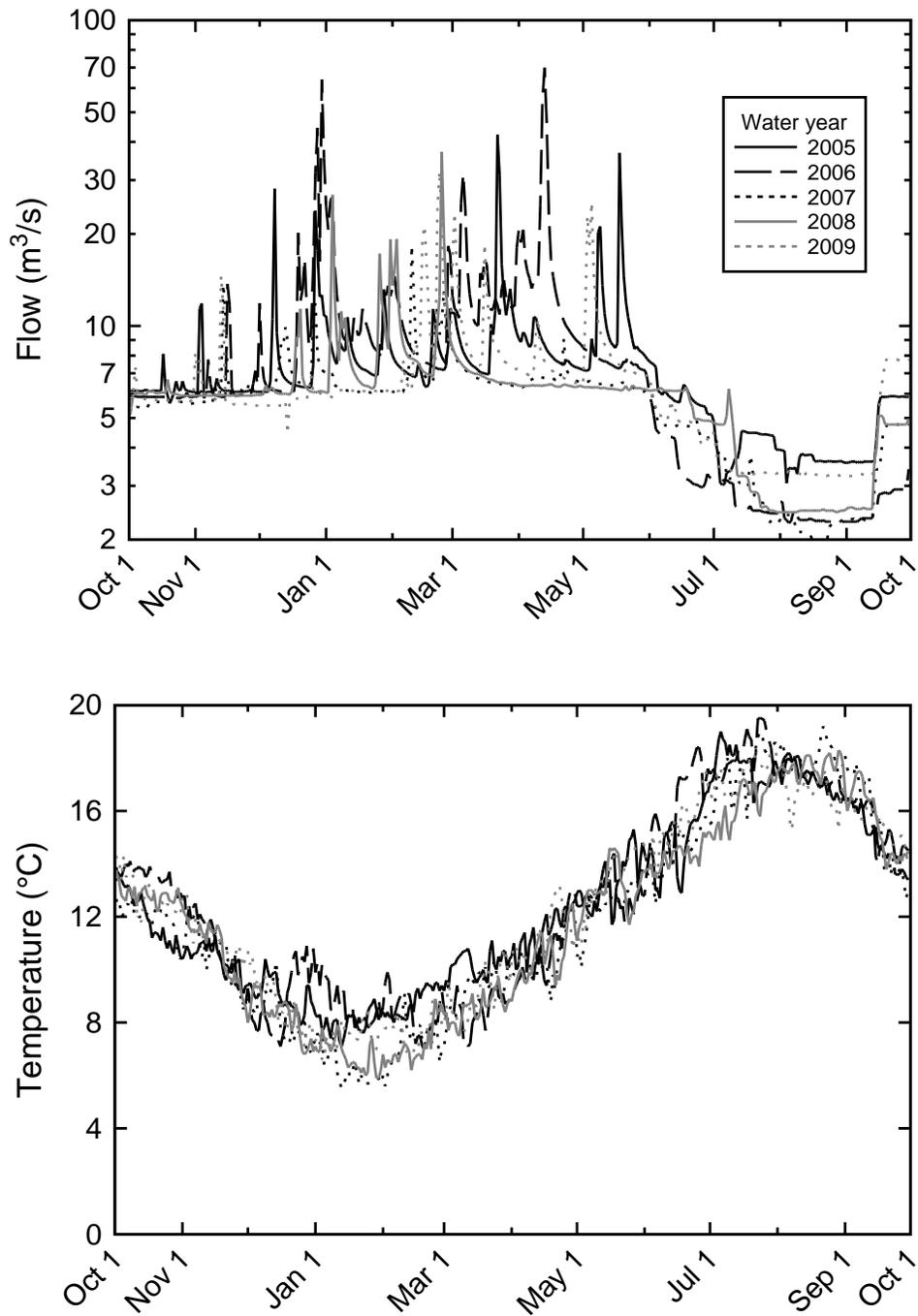


Figure S1. Daily mean flows (upper) and temperatures (lower) for the five simulated years. Temperatures are for the gage at RK 8.3, the middle of six gages in LCC.