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ARTICLE

Effects of Spatial Extent on Modeled Relations between Habitat and Anadromous Salmonid Spawning Success

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Abstract
We address the question of spatial extent: how model results depend on the amount and type of space represented. For models of how stream habitat affects fish populations, how do the amount and characteristics of habitat represented in the model affect its results and how well do those results represent the whole stream? Our analysis used inSalmo, an individual-based model of anadromous salmonid spawning, incubation, and juvenile rearing. The model was applied to 12 sites, totaling 4.0 km in length, on Clear Creek, California, treating the simulated 4.0 km as a synthetic whole stream. Simulation experiments examined responses of anadromous salmonid 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 the effects of flow on the production of large juveniles, varied sharply among sites and varied with spatial extent. Most small sites had little effect on overall results, but one small site provided exceptionally good juvenile rearing habitat and strongly affected the 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. Finally, sites lower in the watershed appear to be more important to model results and anadromous salmonid spawning success because more juveniles migrate through them.

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 (Dunbar et al. 2012). 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 (Williams 1996, 2010a, 2010b; Kondolf et al. 2000; Gard 2005; Ladson et al. 2006).

Several previous studies have developed relationships between spatial extent and the precision or accuracy of instream flow model results (Gard 2005; Williams 2010a). Those studies have, however, 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 as follows: (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

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area each point on a transect represents or by adopting the fully two-dimensional representation of stream area used in hydrodynamic models.

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). Such 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, 2002; Railsback et al. 2009, 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 an anadromous salmonid 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.

In this study we take advantage of the large number of sites to which an anadromous salmonid IBM has been applied on a relatively small stream (12 sites totaling 4.0 km). We treat the 12 sites together as a synthetic "whole" stream, so simulation results for the full 12 sites represent "reality" in the synthetic 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. The first is to quantify the variability among individual sites in model-predicted habitat productivity and examine 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 anadromous salmonid juveniles that migrate downstream out of the simulated stream alive, per female spawner. (Our definition of spawning success therefore also considers rearing 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 is relevant to (but does not directly answer) the study design question of how much stream area should be modeled to predict fish population response to management alternatives with reasonable precision. Our "sites" are two-dimensionally modeled stream segments, ranging in length from 64 m to over 1,200 m, each chosen to represent specific habitat types (explained below).

Our analysis differs in a subtle but important way from previous analyses of spatial extent in the instream flow literature (e.g., Gard 2005; Williams 2010a). Previous analyses were of habitat models that simulated, e.g., the area of "suitable" habitat as a function of flow. Habitat model results for each unit of space (site, transect, or cell) can be treated as independent: habitat "suitability" of one cell does not depend on conditions in other cells (although results are often autocorrelated across space; Williams 2010a). Therefore, bootstrap analysis can be an appropriate approach for analyzing spatial extent effects, e.g., by examining how well different amounts of modeled space represent habitat in an entire stream reach (e.g., Williams 2010a). In our analysis, however, sites are not independent: conditions at one site affect model results for other sites (e.g., the number of juvenile anadromous salmonids migrating into a site from upstream affects the survival and growth of juveniles hatched at that site and the success of juveniles hatched at one site depends on the downstream sites they must migrate through). Our model represents a system of interacting sites, not independent units of space, so bootstrap analysis is not a legitimate (or computationally feasible) analysis approach. Instead, we rely on a more qualitative approach that uses several kinds of simulation experiments.

METHODS

The general approach we used was simulation experiments with inSalmo, an IBM of the freshwater life stages of salmonids: 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 looked at how model results differ when different combinations of sites on the same stream are simulated.

Study Sites

Our simulations used sites on lower Clear Creek (LCC), from the Clear Creek Road bridge at river kilometer (rkm) 14 downstream to the creek's confluence with the Sacramento River (rkm 0), in Shasta County near Redding, California (Figure 1). Lower Clear Creek 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 Wildlife indicate that numbers of fall Chinook Salmon spawning in the upper 7 km of LCC ranged from 3,000 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.

Flow and temperature in LCC are dominated by releases from Whiskeytown Reservoir at rkm 29. Despite the warm Mediterranean climate, the reservoir creates water temperatures of about 6–18°C year-round and flows ranging from 3 to 7 m^3/s, except during runoff events (Figure A.1 in the Appendix). Reservoir releases are typically around 5.7 m^3/s during Chinook Salmon spawning and incubation. The LCC channel is confined by a canyon at its upper end, but downstream from approximately rkm 7.5 it passes through alluvial gravel deposits heavily disturbed by historic gold

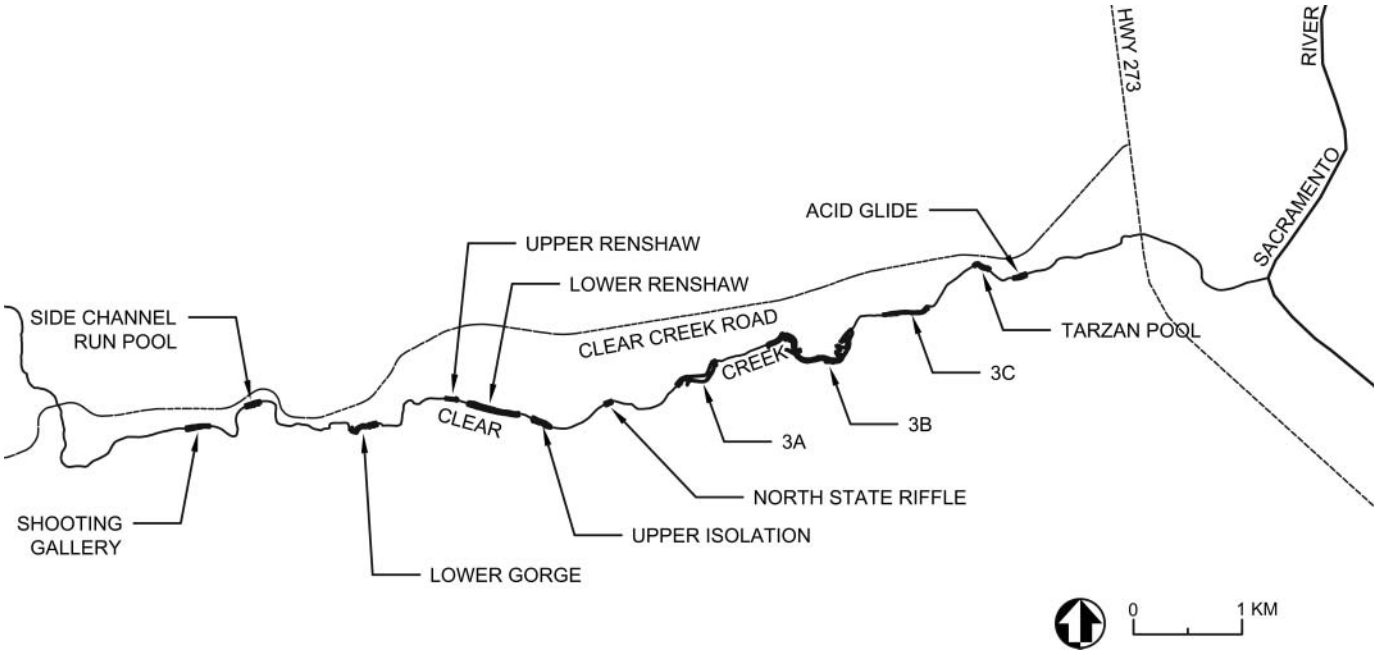

FIGURE 1. Lower Clear Creek, California, flowing from west to east through the 12 study sites.

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 rkm 10.4, and a channel restoration project near rkm 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 Appendix.

Anadromous Salmonid Model

InSalmo is one of a family of IBMs designed for assessing the effects of habitat alteration on stream salmonids; these models have been extensively described and tested (e.g., Railsback et al. 1999, 2009; Railsback and Harvey 2002). We provide a brief overview of inSalmo here and a more detailed description of the model and its application to Clear Creek fall Chinook Salmon in the Appendix. Complete descriptions of inSalmo and the Clear Creek application have been published previously (Railsback et al. 2011, 2013, 2014).

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 as follows: (1) adult arrival and spawning, in which adults are added to the model and they create redds in selected cells, (2) incubation, for which eggs develop at a temperature-driven rate until ready to emerge as juveniles, and (3) juvenile rearing and out-migration. Juveniles select the best cell within a small radius for feeding, a tradeoff between growth and predation risk. Growth depends in part on size-based competition for the available food. 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 "out-migrants" 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 habitat (or, here, the all-sites simulation we use as the "whole" stream; see Simulation Experiment Design below). 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 out-migrants 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.

TABLE 1. Site (model reach) characteristics. The total simulated length is 4,000 m.

Site number and name	Distance from downstream end of Clear Creek (km)	Length (m)	Mean width (m)[a]	Description[b]
1: ACID Glide	2.6	120	23	Juvenile rearing site, glide habitat (moderately deep and fast)
2: Tarzan Pool	3.0	158	24	Juvenile rearing site, pool habitat
3: Restoration 3C	4.3	455	17	Unrestored control site, steep and confined uniform channel
4: Restoration 3B	5.0	1,230	26	Channel restoration site with riffle and pool sequences, juvenile rearing site
5: Restoration 3A (2008)	6.4	519	29	Channel restoration site with riffle and pool sequences
6: North State Riffle	7.5	64	28	Juvenile rearing site, riffle habitat
7: Upper Isolation	8.1	206	33	Spawning site, riffle and run habitat
8: Lower Renshaw	8.6	479	35	Spawning site, riffle
9: Upper Renshaw	9.0	118	28	Spawning site, riffle and run
10: Lower Gorge	10.1	296	19	Spawning site, riffle and pool
11: Side Channel Run–Pool	11.4	139	32	Juvenile rearing site, run and pool
12: Shooting Gallery	12.1	215	25	Spawning site, riffle

[a]Width is at a typical summer flow of 5.66 m^3/s.
[b]See also Figure A.2.

Simulation Experiment Design

Simulation experiments used input for water years 2005–2009, a period with no unusual flow or temperature events but a wide range of spawner numbers (see Appendix). Because simulated Chinook Salmon do not persist from year to year, we treated each simulated year as an independent result. Because this study is focused on the effects of space, not temporal variability, results are reported as the mean over the five simulated years.

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 as follows: (1) out-migrants per spawner (OPS), the number of juveniles that are still alive when they migrate out of the downstream-most site divided by the number of female spawners and (2) large out-migrants per spawner (LOPS), which is identical to OPS but only includes juveniles that are > 5 cm fork length when they migrate out. The LOPS measure is included to evaluate juvenile rearing: the model's newly emerged fry have lengths between 3.5 and 4.1 cm, so out-migrants with a length > 5 cm were able to establish and grow for at least a few days. We present results by simply displaying how these measures varied among the simulation scenarios (including the variation among years), instead of statistically testing specific hypotheses. This approach is used because observing trends and patterns is more meaningful for the general understanding we seek than would be statistical analysis of our particular results. Also, statistical analysis of simulation results can be biased by partially arbitrary decisions, such as how many replicates to execute.

The results of experiments that simulated one or several sites were compared to results from the entire set of 12 sites together. We treat these all-site simulations as a synthetic whole stream, so their results were treated as the "true" responses of the anadromous salmonid population to management variables. The other simulations that most closely matched the all-sites simulation results were considered, for this modeling study, the most accurate models of the "true" 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 out-migrants when they left the reach they were spawned in. All the sites were initialized with the same spawner density; this assumption may not be realistic but it causes differences among sites in simulated spawning success to result from differences in spawning, incubation, and juvenile rearing habitat, not from differences in site length or spawner density.

Instead of just simulating historic conditions, we looked at how simulated spawning success responds to the habitat variables often influenced by river management. This experiment used inSalmo's "limiting factors tool" (Railsback et al. 2011), which automatically generates and executes simulations evaluating the sensitivity of the model results to individual factors. We examined four factors. The base flow analysis added a

constant modifier to daily flow; in five simulations, this modifier had values ranging from −2.0 to +4.0 m^3/s in steps of 1.5 m^3/s (−65% to +70% of the typical 5.7 m^3/s actual flow). (We use the term "base flow" because this experiment primarily affects flow when it is entirely controlled by the reservoir; changes in base flow are equivalent to changes in reservoir release flow.) Similarly, the temperature analysis varied water temperature during the November–May incubation and rearing period by a modifier ranging from −4.0°C to +4.0°C in steps of 2°C (compared to actual temperatures of 8–12°C; Figure A.1). 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; velocity shelter represents cover that reduces swimming effort while drift feeding) from −50% to +50% of 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 (those produced by the all-sites simulations). 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. 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 two, four, six, and nine 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 the simulated response of LOPS to base flow. We examined only LOPS because OPS varied little with flow.

To quantify how well the results from each combination of sites reproduced 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. (Modelers typically have more confidence in trends in results than in absolute predictions, so management decisions are often based on trends. This analysis method removes the absolute differences in results among site combinations and focuses only on differences in trends.) For each site combination, 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.

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 the results of leaving a site out was used as a measure of how strongly the site affects simulated responses.

TABLE 2. Random site combinations for experiment 2, showing the sites included (using the site numbers given in Table 1) and the simulated stream length (m).

Combinations	Sites included	Stream length simulated (% of total length of all sites)
Two sites		
2S-A	6, 12	279 (7)
2S-B	2, 3	613 (15)
2S-C	8, 12	694 (17)
2S-D	1, 5	639 (16)
2S-E	10, 11	435 (11)
Four sites		
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	2,343 (59)
4S-E	4, 5, 7, 10	2,251 (56)
Six sites		
6S-A	1, 4, 9, 10, 11, 12	2,119 (53)
6S-B	3, 6, 7, 8, 9, 10	1,618 (40)
6S-C	3, 4, 7, 10, 11, 12	2,541 (64)
6S-D	3, 4, 6, 7, 8, 12	2,649 (66)
6S-E	2, 3, 4, 5, 7, 10	2,864 (72)
Nine sites		
9S-A	1, 2, 4, 5, 6, 7, 8, 10, 11	3,211 (80)
9S-B	2, 3, 4, 5, 6, 7, 8, 9, 12	3,445 (86)
9S-C	1, 4, 5, 6, 7, 9, 10, 11, 12	2,908 (73)
9S-D	2, 3, 4, 5, 6, 8, 9, 10, 12	3,534 (88)
9S-E	1, 2, 3, 4, 6, 7, 9, 10, 12	2,863 (72)

The system response used in the experiment was the effect of base flow on LOPS.

RESULTS

Variation Among Sites at Baseline Conditions

Simulation results for OPS were generally consistent among sites, with all but one site having a median OPS between 2,800 and 3,500 (Figure 2, top panel). The Tarzan Pool site had a much lower OPS than the others. Spawning gravel is sparse at that site, resulting in high superimposition mortality (84% of eggs).

Two processes explain this consistency. First, egg mortality was consistent among sites. The primary source of egg mortality was superimposition of new redds over old ones, causing 40–50% egg mortality. Superimposition rates are largely driven by the availability of spawning gravel, which is

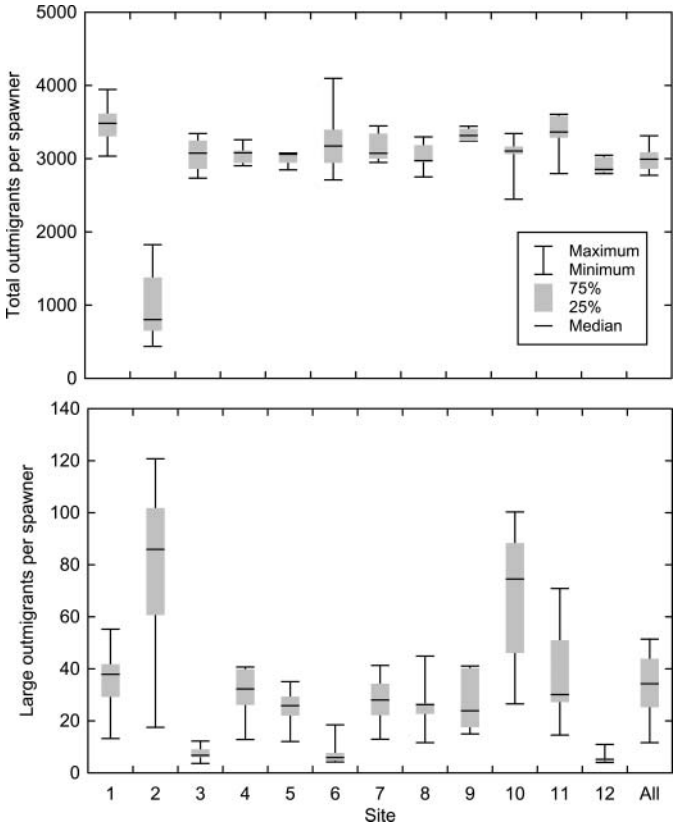

FIGURE 2. Numbers of total (upper panel) and large (fork length > 5 cm; lower panel) out-migrants from simulations of each site by itself. Sites are identified by their number given in Table 1; values labeled "All" are from simulations including all sites. Plots represent the distribution of results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

relatively abundant throughout LCC. Mortality related to temperatures below or above optimal was also consistent among sites because temperature regimes differed little among sites. Second, a very high percentage of newly emerged anadromous salmonid 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 indicates that fewer than 1 juvenile in 100 stayed long enough to reach 5 cm in length. Hence, few out-migrants were affected by any differences among sites in rearing habitat.

The results for large out-migrants were more variable among sites (Figure 2, lower panel). In fact, the site with anomalously low OPS (Tarzan Pool) was one of two with the highest LOPS. 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 LOPS results 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 LOPS, but one of those sites (North State Riffle) had very low LOPS and one site with high LOPS (Lower Gorge) was intended to represent spawning habitat.

The baseline simulations including all sites (Figure 2) differed from the individual-site simulations because juveniles in them had to migrate through all the downstream reaches before being counted as successful out-migrants. These simulations produced a OPS value that was 99% of the sum of OPS over the individual-site simulations, indicating that (in these simulations) mortality during out-migration was minor. The all-sites simulation produced LOPS of 111% of the sum over individual-site simulations, indicating that growth during downstream migration could have at least modest effects on LOPS. The two sites with the highest LOPS 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%, respectively, of the mean across sites. This result indicates that juveniles that hatched upstream also took advantage of the rearing habitat in these sites.

Experiment 1: Responses of Individual Reaches to Habitat Variables

Base flow.—The OPS showed little consistent response to base flow (Figure 3, upper left panel), with a value of about 3,000 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 OPS 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 anadromous salmonids migrate downstream very soon after emerging from their redds and hence are not affected by feeding habitat conditions.

The LOPS was more sensitive to flow and more variable among sites (Figure 3, lower left panel). At the sites producing the highest LOPS, LOPS decreased by as much as 70% as flow increased. At sites where LOPS was low (North State Riffle, Restoration 3C, Shooting Gallery), it was steady or even increased as flow increased.

The response of LOPS 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 LOPS closer to the "true" values produced by simulating all sites. (However, Restoration 3B produced a different trend, with LOPS increasing slightly at the highest flows.)

Temperature.—The simulated variation in water temperature produced a strong, nonlinear response in OPS that was

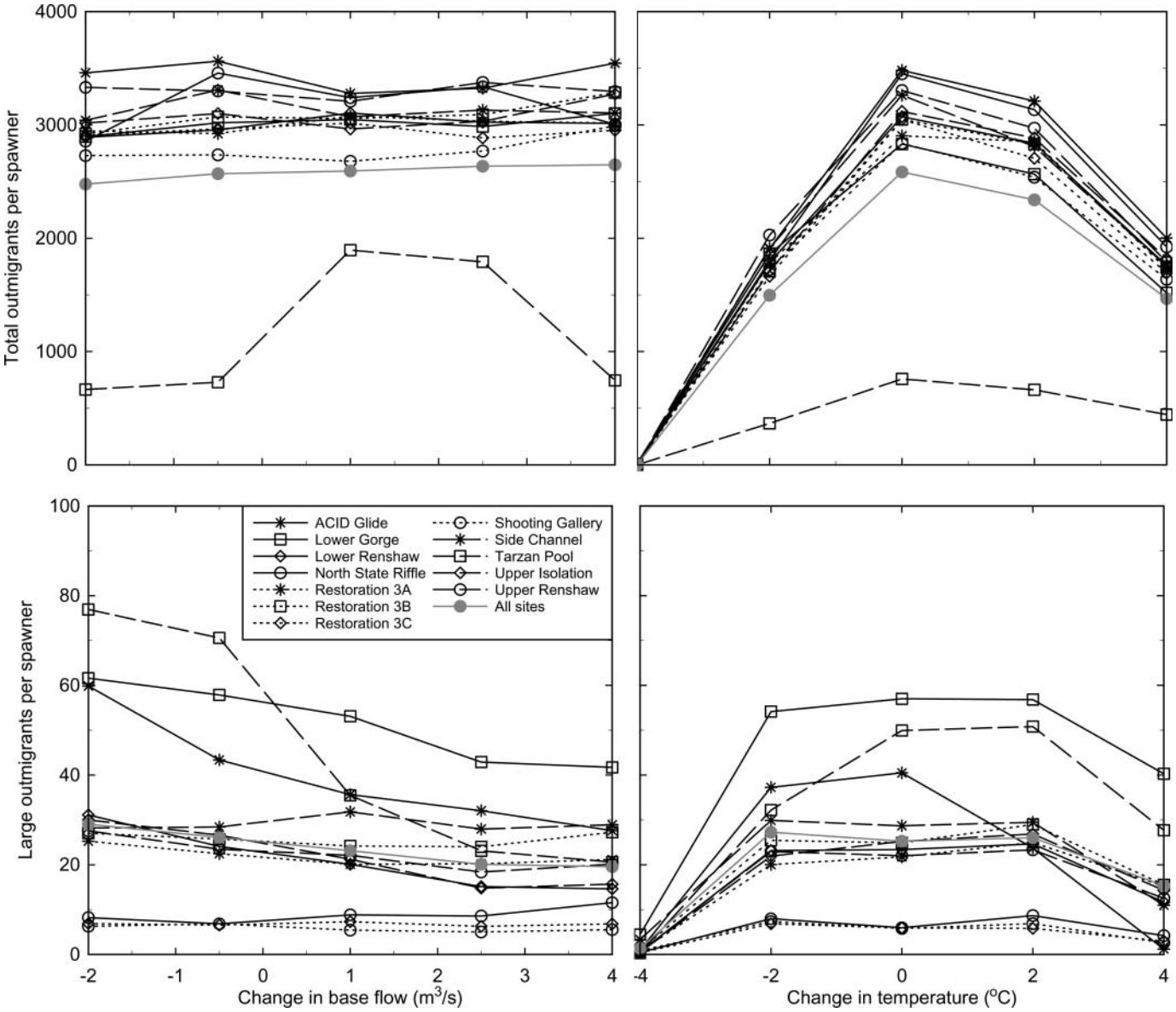

FIGURE 3. Simulated response of spawning success to base flow (left panels) and temperature (right panels) at each individual site by the total number of out-migrants per spawner (top panels) and the number of large (fork length > 5 cm; bottom panel) out-migrants per spawner. Results are the mean over five simulated years under each flow or temperature scenario.

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 increases as temperatures depart from a range of optimal temperatures that happens to coincide with the 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 LOPS to temperature clearly reflected egg mortality but was more complex and variable among sites (Figure 3, lower right panel). The level of LOPS was lowest at the lowest and highest temperatures, but the temperature change producing the highest LOPS varied among sites. Several processes could explain the different responses. First, temperatures during fry emergence (January–March; Figure A.1) 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 (Railsback and Harvey 2002; Harvey and Railsback 2007), 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 OPS or LOPS (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 the observed levels (>100% relative availability) sharply decreased superimposition mortality of eggs and, hence, increased the production of out-migrants.

Velocity shelter availability.—The availability of velocity shelter for drift feeding had no consistent effect on OPS at any sites, but LOPS increased with increasing 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 the most large out-migrants, the small sites varied widely in response, and the largest sites each produced results closely following (in both trend and magnitude) the LOPS 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

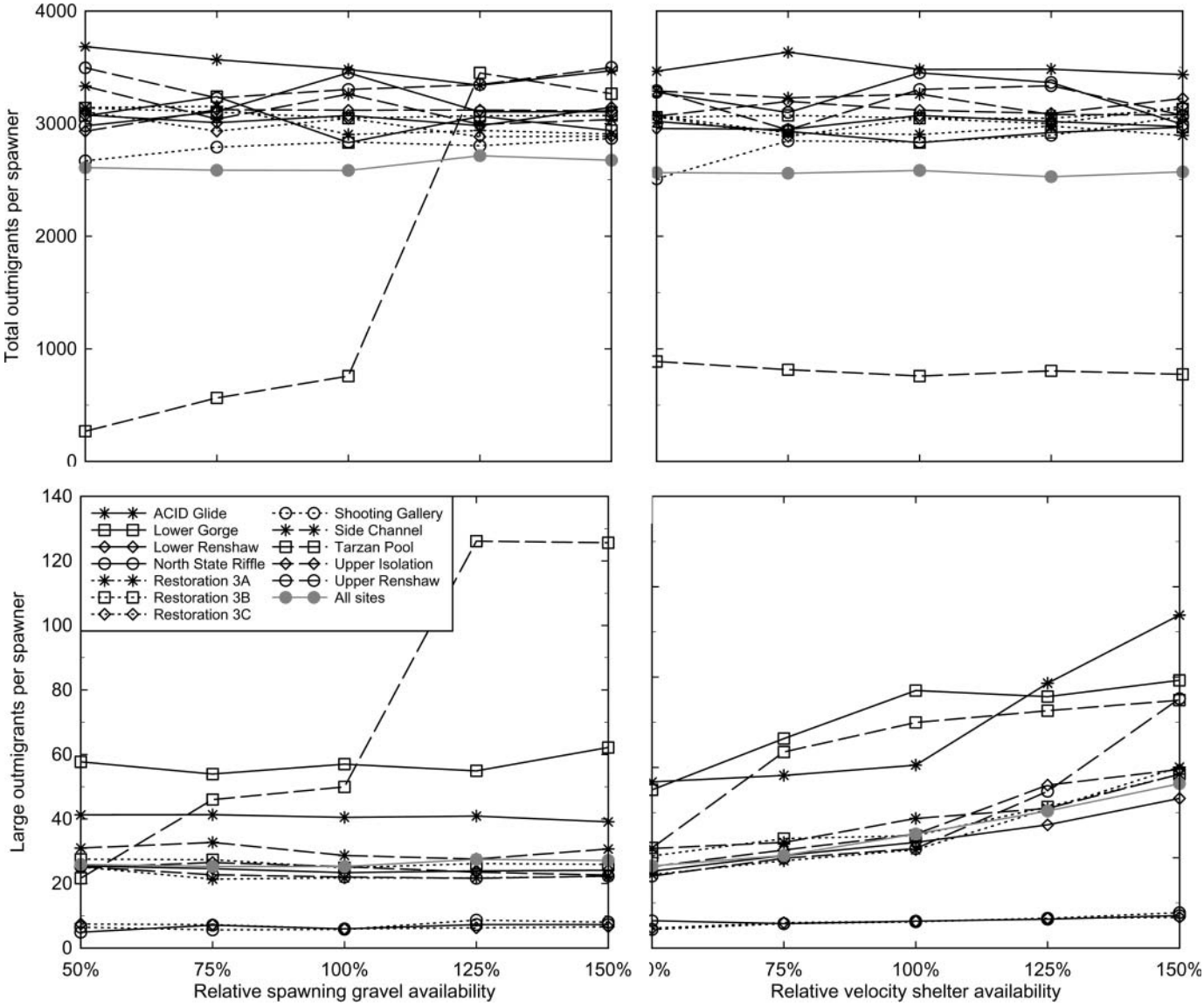

FIGURE 4. Simulated response of spawning success to the availability of spawning gravel (left panels) and velocity shelter (right panels) at each individual site by the total number of out-migrants per spawner (top panels) and the number of large (fork length > 5 cm) out-migrants per spawner (bottom panel). Results are the mean over five simulated years under each scenario.

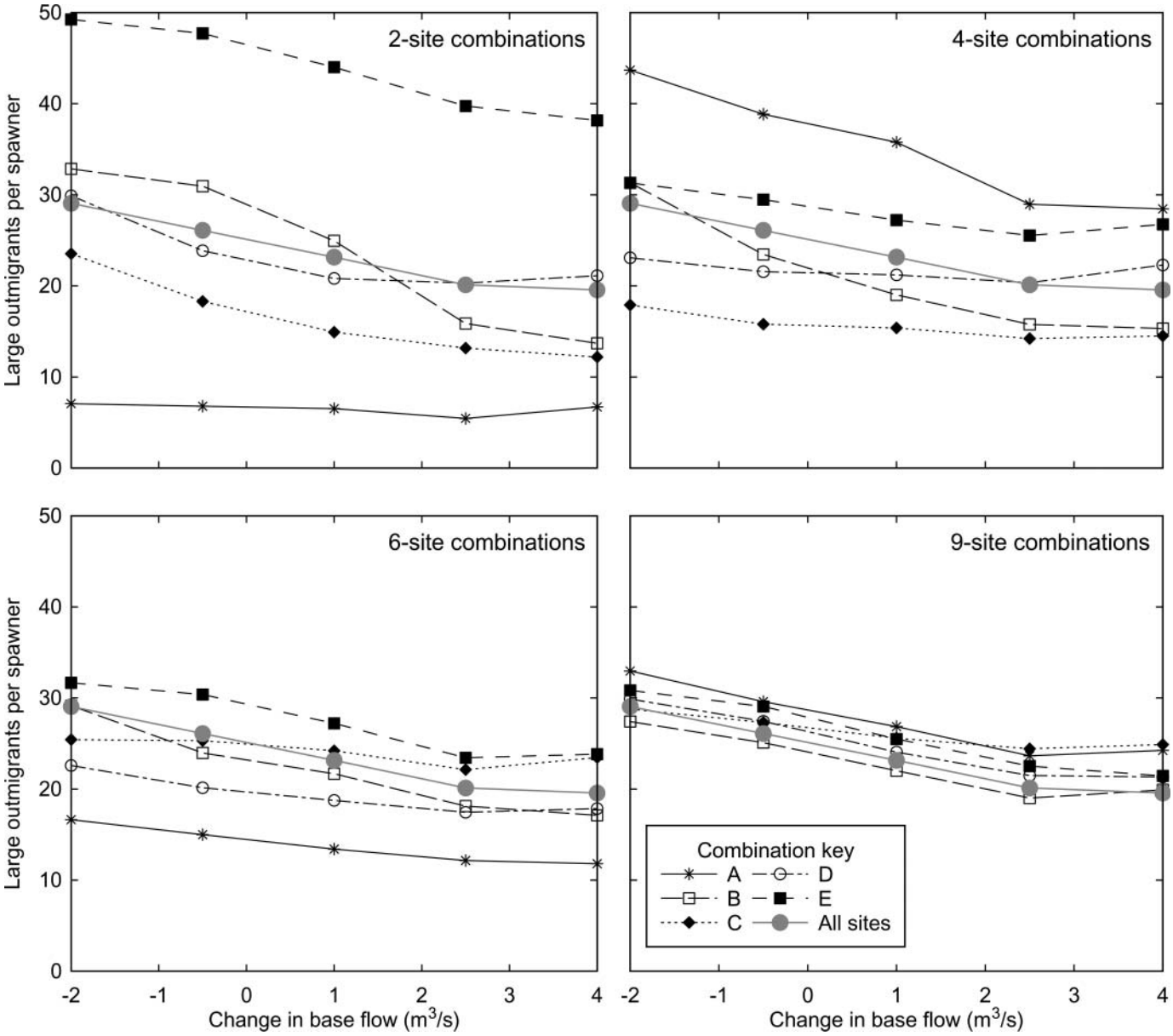

FIGURE 5. Results from the multiple-site experiments, showing the response of spawning success to base flow. Results are the mean number of large outmigrants per spawner over five simulated years. Each panel displays the results of five site combinations, which are defined in Table 2. For reference, each graph also displays the "true" results obtained from simulating all 12 sites together.

(2S-A, 4S-B) reproduced the general pattern of LOPS decreasing as flow increased, up to the fourth flow scenario (base flow increased by 2.5 m^3/s) (Figure 5). The deviation from the "true" results (from simulating all 12 sites) generally decreased as more sites were included.

The RMSE values representing the difference in trend from the "true" results (Figure 6) are relatively small, less than about 10% of the LOPS values reported in Figure 5 for combinations of four or more sites. They indicate no simple relationship between length of stream simulated and simulation accuracy, except that the combinations including > 3,000 m of stream (out of the 4,000-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 the all-sites results (Upper Renshaw) was one of the shortest sites and intended just to represent spawning habitat (Table 1).

The Tarzan Pool site may be important for how closely a site combination matched "true" spawning success. This site is small, yet it produces high values of LOPS (Figure 2) and is near the downstream end of LCC, where almost all outmigrants move through it. (Results of Experiment 3, below,

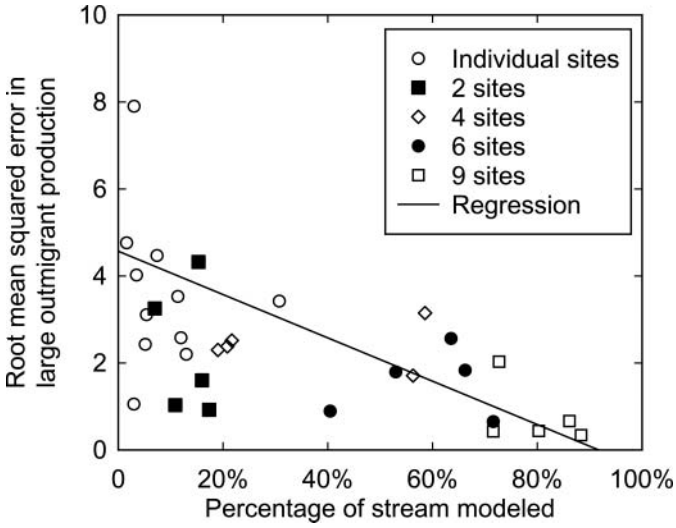

FIGURE 6. Root mean square error (RMSE) in the simulated response to changes in base flow after removing the mean difference between site combinations and the "true" all-site values. Each point represents one of the site combinations in Table 2 and Figure 5 or one of the individual sites (Figure 3, lower panel). The *y*-axis is the RMSE in the number of large out-migrants per spawner across the five flow scenarios, indicating the difference in the trend of response to flow from the "true" values. The *x*-axis is the percentage of the total length of stream simulated as given in Table 2. One individual site (Tarzan Pool) is not displayed as it had a RMSE of 20.3 out-migrants/spawner.

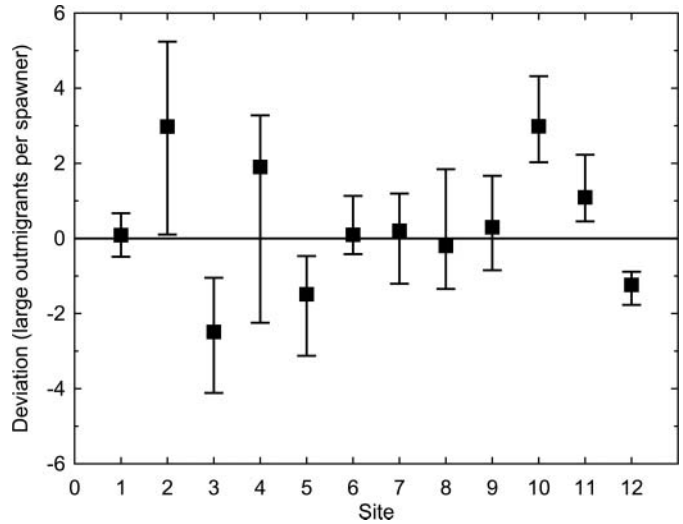

FIGURE 7. Effect of individual sites on the simulated response of lower Clear Creek spawning success (as the mean number of large out-migrants per spawner over five simulated years) to base flow. The *y*-axis represents the effect of individual sites (indicated on the *x*-axis) on simulations of the entire lower Clear Creek system, that is, 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). The sites are identified by their number given in Table 1.

indicate that sites lower in the stream generally had stronger effects on the results, though we cannot be sure whether this was an effect or coincidence.) Of the six-site combinations, the one that included Tarzan Pool (6S-E) had much lower RMSE than the others. Only one of the nine-site combinations (9S-C) did not include Tarzan Pool and it was the only one with a RMSE above 0.7. On the other hand, the two-site combination including Tarzan Pool (2S-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 the response of LOPS, leaving out 1 of the 12 sites 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 the mean LOPS 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 with small ranges of effects had little influence on the 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 LOPS, confirming it as a "hot spot" for large out-migrant 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 out-migrant production and also strongly affected the response shape, indicating that they are especially important for predicting the response of the entire system.

DISCUSSION

How important is the amount of space represented in a stream fish model to the results used to support river management decisions? There is of course no simple answer to this question because every river and every model is different. We studied just one stream, simulated with a model that includes some but not all of the complexities of real anadromous salmonid populations. However, 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 unusual level.

Study Limitations

Our study has several limitations 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 5 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; evidence of this is that the one site lacking abundant spawning habitat, Tarzan Pool, responded to flow and gravel availability much differently than the other sites.

We also reiterate that, because sites are not independent in inSalmo, we could not use standard bootstrap analysis as a tool for understanding the effects of spatial extent on model results. For this reason and because of computational limits, our analysis uses approaches—small numbers of site combinations selected without replacement, qualitative instead of quantitative analysis—that are not standard for bootstrap analysis. Finally, we remind readers that we treated 4,000 m of simulated stream as "reality," so our results are not directly applicable to the full 14 km of LCC.

Comparison to Previous Analyses

It seems valuable to compare our results and conclusions with those of previous studies of how the spatial extent of stream management models affects model results. The two most prominent previous studies (Gard 2005; Williams 2010a) examined the question of how the number of "transects" used in a one-dimensional Physical Habitat Simulation (also known as PHABSIM) analysis affect results. These studies both used the same set of 107 transects to represent the "whole" stream and bootstrap-type analysis to examine how key results varied with the number of transects. These two studies, like ours, indicated that the variability in results decreases as more space is modeled, but unfortunately it does not seem possible to make more meaningful comparisons between those studies and ours. A transect is a one-dimensional depiction of habitat and therefore represents no space; as Williams (2010b) points out, there are infinite transects that could be placed in any length of stream. Therefore, our results, such as those in Figure 6, cannot be compared to the results of Gard (2005) and Williams (2010a) in the absence of an assumption about how much space each of their transects represents. These two previous studies, like ours, also refrained from making specific recommendations about how much space is "enough."

Effects of Spatial Extent

Some simulated anadromous salmonid population responses were insensitive to spatial extent. Our primary example was OPS: 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 (1) spawning gravel was abundant and (2) the vast majority of such juveniles migrated downstream immediately after emergence and hence were minimally 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. For example, LOPS varied widely among sites, as did its response to habitat variables such as flow and temperature. Increasing base flow, for example, produced lower LOPS overall but the response at some sites opposed this overall trend.

Given the 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 LOPS. These are short sites, except Lower Renshaw. Lower Renshaw had little effect on the 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 the results? Our third experiment identified two sites, Restoration 3B and Tarzan Pool, as having the strongest effects on the shape of the simulated response of LOPS 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, LOPS 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 the most effects on the results but apparently for a third reason: LOPS was unusually low 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 that produced results (Figures 3, 4) most similar to the results for all sites combined 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 Anadromous Salmonid Spawning Success

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 out-migrants. If we had analyzed inSalmo results only for the number of out-migrants of all sizes, we would have concluded that spatial variation and model extent was relatively unimportant. However, the production of out-migrants 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 the 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 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 LOPS 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 that represent 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 the results are representative (Williams 2010a). Our experiment indicates that this strategy requires a relatively large spatial extent to make high representativeness likely, especially when small areas of especially productive habitat (hot spots; here, Tarzan Pool) have large effects on the results. The second strategy is to combine 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 problem with this approach is the need to identify hot spots and especially representative areas before modeling starts. Spatial extents may need to be substantially greater than those of typical instream flow studies to represent an entire stream well, capture the effects of especially good or bad habitat, and avoid bias due to how sites are selected.

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Appendix: Detailed Model Information

Summary Model Description

Model scales.—InSalmo operates at a daily time step. Model runs start at the time that adults first arrive from the ocean and end at a date when all juveniles have typically either died or migrated downstream; the simulations here run for 1 year starting on October 1. (Multiyear runs are possible, but because the juvenile Chinook Salmon we simulate are gone before the next year's brood appears, each brood year is independent.)

Habitat is depicted at two spatial scales: reaches and cells. A reach represents a length of stream, typically several hundreds of meters 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. Food production rates (drift food concentration and benthic food density) are static reach variables; the simulations here use the same values for all reaches. Each reach is made up of many cells, irregular polygons that each have their own depth, velocity, food availability (a function of reach food parameters and the cell's area, depth, and velocity), and cover availability for drift feeding and predator avoidance. The spatial resolution (minimum cell size, approximately 1 m^2) was chosen as approximately the area used by one fish (super)individual to feed under typical drift-feeding conditions.

InSalmo represents the stream life stages of anadromous salmonids: adults starting at the time they arrive from the ocean via upstream migration, the redds created by spawning adults, and juveniles from the time they hatch through when they move down out of the simulated stream. (Smolting and differences between pre- and postsmolting juveniles are not represented.)

To make model execution speed reasonable, juvenile anadromous salmonids are represented as "superindividuals": each individual in the model represents 20 fish. This superindividual size has negligible effects on the 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 the 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. During incubation, eggs are vulnerable to mortality due to superimposition (creation of a new redd at the same location), extreme temperature, disease, and desiccation if the cell is dewatered. For each of these redd mortality sources, the daily mean egg survival rate is a deterministic function of habitat variables and model events, such as the temperature and whether the redd's cell was dry. Superimposition is a particularly frequent cause of redd mortality in our simulations; the egg survival rate decreases with the density of new redds (redds per cell area) created each day. The number of eggs surviving each type of mortality is then a stochastic function of the mean survival rate. When the development period is complete, surviving eggs are turned into new superindividuals representing juvenile anadromous salmonids.

Juvenile rearing and out-migration.—On each simulated day, juveniles select a habitat cell to feed in or else decide to migrate downstream, feed and gain or lose weight, and undergo mortality risks.

Simulated juveniles select their habitat cell for feeding from nearby cells within a radius that increases with fish size but always includes at least 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). Normally, juveniles select the cell offering the lowest risk from those offering positive growth; however, very young fish without access to moderate velocities ($<\sim$50 cm/s) experience negative growth and a high risk of mortality due to energy depletion. Juveniles decide to migrate downstream if the expected future survival and growth in the 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 "out-migrants" and removed from the model. Hence, out-migrant results from the model refer to juveniles that have moved downstream through all the simulated reaches below their natal reach.

Growth is 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. However, growth depends on food availability, and inSalmo represents competition among juveniles for the daily food available in each cell. This competition is a size-based hierarchy: juveniles select their habitat in size order, with smaller fish having access only to the food not already consumed by larger fish in the same cell. Hence, density-dependent phenomena (growth, survival, migration) emerge from characteristics of the habitat and fish population.

The mortality of juveniles is simulated as a random Bernoulli trial for each of several kinds of mortality, with the daily probability of surviving each being a deterministic function of the fish's state and its habitat. Starvation and disease risk varies with the fish's condition (weight relative to length). For juveniles able to obtain positive growth, the major causes of mortality are two kinds of predation. The risk of predation by fish is assumed high except in cells with low depths or abundant hiding cover and decreases as juvenile length increases. The 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 anadromous salmonid spawning success were intentionally left out of inSalmo to avoid additional complexity. These include the following: (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). (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 out-migration methods still result in many fry moving rapidly downstream because velocities exceeding their swimming ability produce rapid weight loss and high mortality risk. (5) Postjuvenile life stages and population dynamics: our simulations do not represent juveniles after they migrate out of Clear Creek or provide feedback of spawning success on adult abundance in subsequent years. Hence, results for 1 year are independent of results from previous years.

Input Development

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 20–80 observations/100 m^2 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-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 (1.4–25.0 m^3/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 1,400 m^3/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 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 sites vary widely in hydraulic characteristics at typical flows (Figure A.2). Many have large areas of shallow, slow habitat while others have little, some are distinctly riffles and runs (low–medium depth and higher velocities) and others pools (large areas of high depth), and the longer reaches tend to have diverse hydraulic conditions.

The third step was developing values for each cell's habitat variables: the fraction of cell area with spawning gravel, the 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 was gravel suitable for Chinook Salmon spawning (diameter 1.5–8.0 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 (1) had velocity at least 40% lower, (2) had depth > 10 cm (assuming fish would not feed in extremely shallow habitat), and (3) 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 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 m^3/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 m^3/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 gauge on Clear Creek near Igo (USGS 11372000), upstream of our sites at rkm 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 rkm 7. Turbidity data were

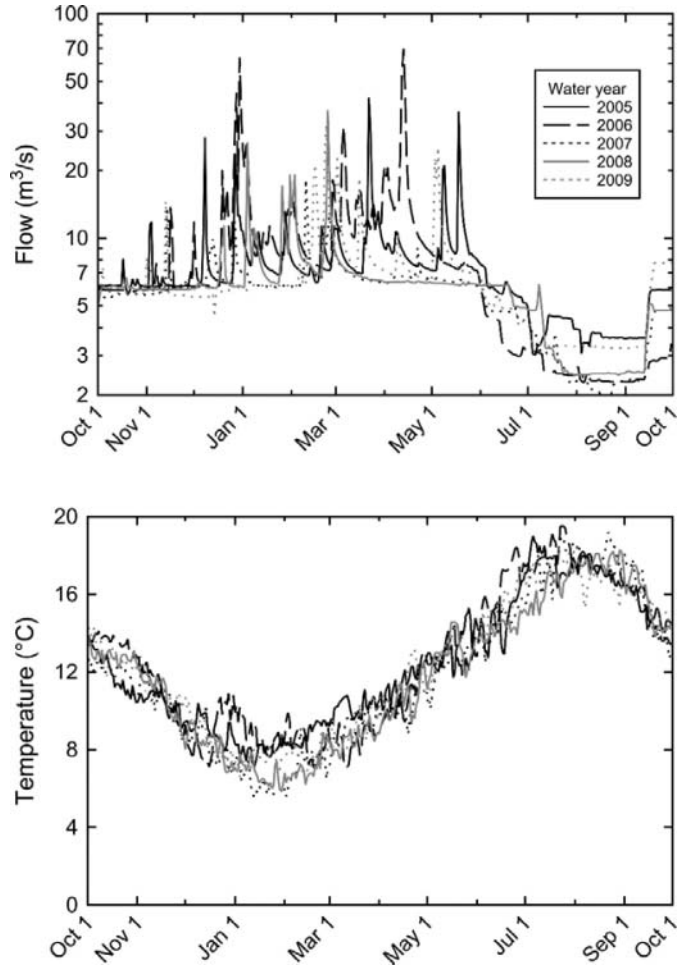

FIGURE A.1. Daily mean flows (upper panel) and temperatures (lower panel) in lower Clear Creek for the five simulated years. Temperatures were observed at river kilometer 8.3.

collected during water years 2003–2007, allowing computation of daily mean turbidity for 534 d. Using linear regression, flow at the Igo gauge 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 m^3/s (August) to 9.7 m^3/s (March), and flow is never less than 2.0 m^3/s (Figure A.1). The period includes only 19 d with flow above the approximate channel-filling value of 25 m^3/s, and the highest flow is 70 m^3/s. Over all days and inputs, temperature (Figure A.1) is always between 5.3°C and 21.7°C, with a mean of 12.1°C. Only 0.6% of values are above 20°C (all occurring at gauges downstream of that used for Figure A.1). Monthly mean turbidities are < 5 NTU for all months, and only 13 d have turbidity > 20 NTU.

The characteristics of the spawner population were input for each simulated year and reach. For all sites and years, adult

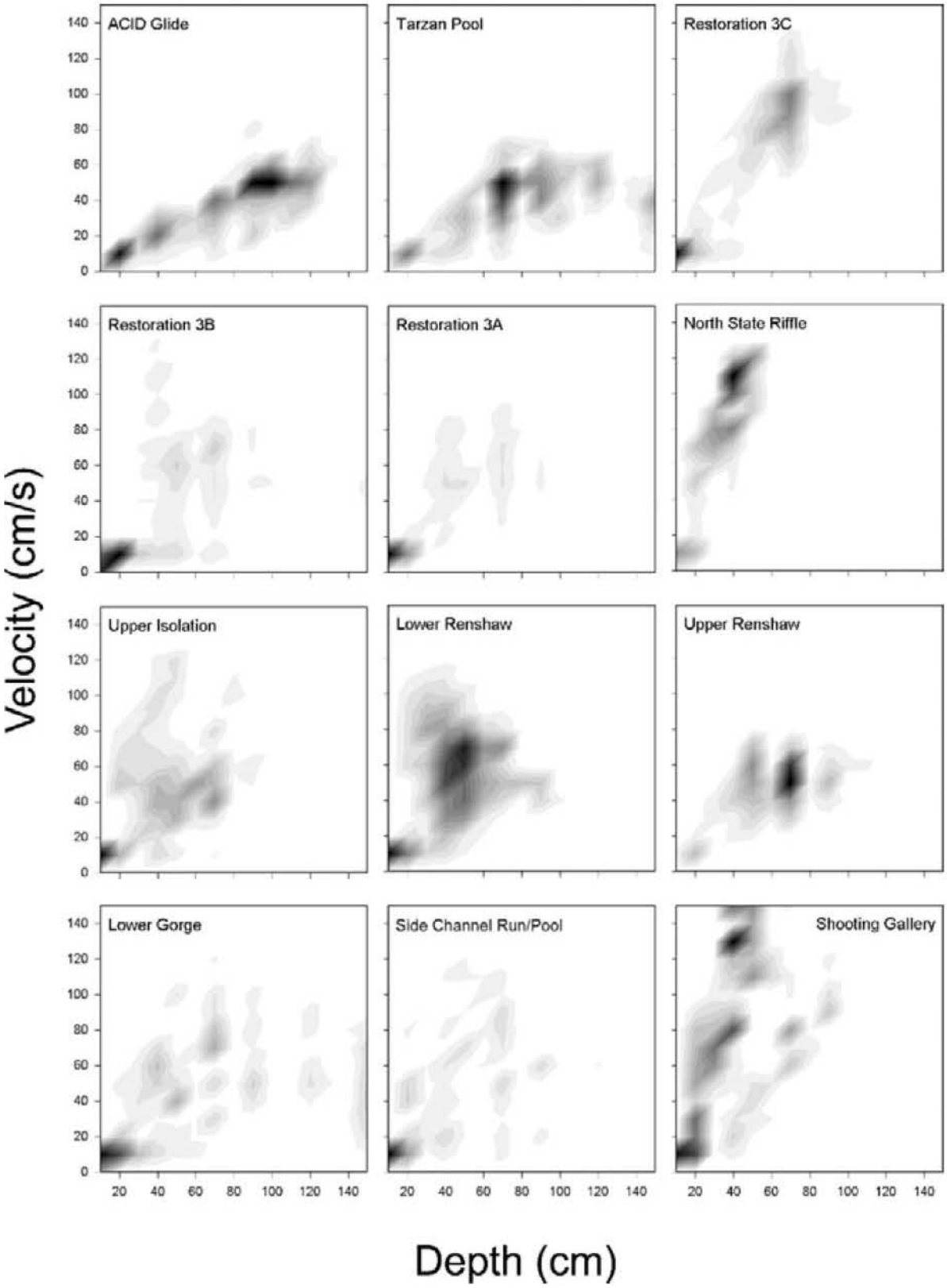

FIGURE A.2. Depth and velocity distributions of the 12 model reaches at a typical flow of 5.66 m^3/s. The areas of model cells were arranged into 10-cm depth and velocity bins using a histogram, and the histogram values were contour plotted. Darkness is linearly scaled to the percentage of reach area in each combination of depth and velocity bin.

TABLE A.1. Annual anadromous salmonid spawning population characteristics that were used to initialize inSalmo.

Year	Spawner density (number/km)	Percent female
2005	2,120	65%
2006	1,210	57%
2007	590	64%
2008	1,100	65%
2009	460	57%

spawners were assumed to arrive at the sites during October 2–30, with lengths drawn from a normal distribution with a mean of 85 cm and standard deviation of 8.1 cm (lengths less than half the mean were redrawn). The number of adults arriving at each reach was calculated by (1) keeping spawner density (number per kilometer of 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 A.1). 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 (1,200 spawners/km). Our methods for specifying spawner abundance mean that model results do not reflect differences among sites in spawner density nor give any feedback from the spawning success in 1 year about the 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 the parameters representing the food availability and the risk of predation by fish and terrestrial animals and the function relating out-migration to juvenile length. Calibration objectives were to match several patterns observed in data from an out-migrant 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 out-migration, (3) date on which mean out-migrant length exceeds 5 cm, and (4) maximum out-migrant 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.

APPENDIX REFERENCES

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