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A salmonid individual-based model as a proposed decision support tool for management of a large regulated river

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Abstract. Large regulated rivers often require fisheries and water managers to make management decisions involving resident fish population dynamics that have many ecological drivers. Because of the large scale of the system and often competing interests and demands for water, there is a critical need for decision support tools (DSTs) that allow examination of alternative management scenarios while considering key ecological interactions. Spatially explicit individual-based models (IBMs) can serve as effective DSTs by providing information on fish population dynamics while accounting for, and providing extensive, spatially explicit information on, the numerous ecological drivers. Spatially explicit IBMs are often difficult to implement owing to the numerous and often complex inputs the models require. Here, I demonstrate how a suite of free, graphical user interface equipped programs, along with three custom-built and publicly available plugins, can streamline the modeling process and serve as a IBM-based DST for fisheries management on large regulated rivers. The main program is a spatially explicit IBM of juvenile salmonid dynamics, inSALMO, with two other programs that generate the key input data in the required spatially explicit formats. I then use this proposed DST to simulate a Chinook salmon population on a portion of California's Sacramento River to determine whether an IBM-based DST is appropriate to evaluate management impacts on a large regulated river. The Sacramento is a large river of major concern in California and is representative of many rivers in the United States and worldwide in that it is dammed, has a resident fish population, and is heavily used for water supply. The proposed DTS results compare favorably with the predictive power of a general additive model, while providing a much fuller and richer data set that could significantly aid and inform management decisions.

Key words: Chinook salmon; dams; decision support tools; endangered species; individual ecology; individual-based models.

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INTRODUCTION

The majority of North America's large rivers have one or more dams which regulate flows for management reasons (Dynesius and Nilsson 1994). Evaluating the impacts of dam operations on downstream water temperature, flow, and ecological communities is difficult because of the wide range of interacting factors. For example, North American anadromous and riverine fish populations in regulated rivers are threatened from high temperatures and altered flows (Mantua et al. 2010), as well as structural habitat loss and thermal habitat loss from anthropogenic climate change (Katz et al. 2013). These threats interact with each other as well as other ecological drivers in complex ways, resulting in different effects on different fish populations (Crozier and Zabel 2006).

Depending on the system, humans have varying levels of control over these ecological drivers. All storage dams allow for the control of the timing and rate of water release, and several have systems that allow direct control of release temperatures, such as Glen Canyon Dam on the Colorado River, Cougar Dam on the McKenzie River, or Flaming Gorge Dam on the Green River. Even dams without direct temperature control systems can have some control over river temperature through release timing and patterns (Krause et al. 2005). Managers also have limited control over quality of habitat downstream of dams through restoration efforts. These restoration efforts may have different effects depending on their composition, size, and location. For example, substantial resources are put toward adding gravel to increase salmon spawning habitat in sediment-starved rivers below dams; however, there is often little effort to quantify the benefits of these costly actions, particularly the interactions with other key factors such as flow and temperature (Zeug et al. 2013). These complex interactions between ecological drivers and the limited management options highlight the need for decision support tools (DSTs, a system which is designed to solve ill-structured problems, has easy to use and powerful interface, can combine models with data, can explore alternatives in the solution space, can supporting different decision-making methods, and allows for interactive and recursive problem-solving; Sullivan 2002) for regulated river management. These DSTs should consider numerous ecological drivers, and be spatially explicit to account spatial interactions between hydrology and habitat, and the location of restoration efforts. One of the challenges of spatially explicit DSTs is making them general enough so they can cover a range of systems while maintaining a streamlined modeling process.

An individual-based model (IBM) framework may be appropriate as a DST because of the complex and spatially explicit nature of these systems as well as the range of potential impacts managers need to consider. For ecological problems, IBMs have a number of significant advantages: (1) They can model very complex systems with numerous environmental inputs both natural and anthropogenically controlled, (2) they can be spatially and temporally explicit, (3) they allow the inclusion of many biological processes and analysis of the parameters that describe those processes, and (4) they can reveal the mechanism by which a parameter or environmental driver may affect the behavior of the system, not simply the final effect on the system. Additionally, IBMs also allow for complex phenomena to emerge from the model, which may be important for managing the system successfully (DeAngelis and Grimm 2014). Individual-based models have successfully modeled fish community responses to management actions in rivers and lakes (McDermot and Rose 2000, Railsback et al. 2013), but to date, not for large managed rivers. Individual-based models and models that focus on individuals have been applied to large regulated rivers, but not in a manner that could model fish community responses to numerous potential management actions (Petersen and DeAngelis 2000, Reed et al. 2011, Bates et al. 2014). One of the impediments to this application at this scale is the large and complex data requirements of a salmon IBM.

To examine the potential usefulness of IBMs as DSTs for salmonids and water management on large regulated rivers, I modified and linked a suite of tools to form a DST and then compared the results to field data on the upper portion of the Sacramento River, California. The suite of tools consists of three free, graphical user interface (GUI) equipped programs and three custom, publically available plugins (easily installed additions to a program) which together form a free, GUI-based DST. The IBM program in this software set is inSALMO, while the two supporting programs are HEC-RAS 5 (Hydrologic Engineering Center 2016) and QGIS (QGIS Development Team 2016) with custom plugins. This set of programs allows for a streamlined modeling process which still accounts for numerous ecological drivers in a spatially explicit manner.

The Sacramento River is the largest river in California (mean annual flow = 797 m^3/s) and is similar to many North American rivers in several ways. Like 43 of North America's 74 large rivers (mean annual flow over 350 m^3/s), the Sacramento is dammed (Dynesius and Nilsson 1994). It is also fragmented and heavily used for urban and agricultural water supply. Like the several large dams mentioned above, the Sacramento's largest dam (Shasta Dam) is equipped with a temperature control device, which allows for selective withdrawal from different depths in the thermally stratified reservoir. Finally, salmon-related concerns help drive watershed management decisions in the Sacramento Basin; as it does in 56,000 km^2 of watershed in OR, WA, and CA (NOAA 2010).

As inSALMO had not yet been implemented for a fish populations in a river system this large, my first step was to determine whether the program generated reasonable results for the early life stages of Chinook salmon (*Oncorhynchus tshawytscha*) on the upper portion of the river where dam operations have a strong influence on temperature and flow. I looked at winter-run Chinook salmon spawner to smolt survival rates and smolt production on the upper 96 km of the Sacramento River and compared my simulated results to 18 yr of field data. As a benchmark for model performance, I compared the IBM results to both a linear model and generalized additive model (GAM). This comparison is simply to show how other more classical models perform on this system.

The IBM structure of the DST allowed me to generate results from an individual scale to an annual cohort scale. The model results were variable across scales, with some phenomena apparent on one scale while their corollary was missing on other scales. The results indicate that predation and redd superimposition were the largest causes of juvenile mortality in the system and that turbidity reduced predation pressure. The DST also indicated that as the number of juvenile salmon increased, the fraction of large juveniles decreased. Results and simulations similar to these are the type of information and tests that managers need to make informed management decisions on large regulated rivers.

Materials and Methods

Railsback et al. (2013) previously described inSALMO in the "overview, design concepts, and details" format (ODD), so I will only briefly describe inSALMO here. inSALMO assesses management actions, such as flow conditions or habitat augmentation, on the freshwater life stages of salmon. It runs on a daily time step. There are three biological entities for salmon in the program (adults, redds [a group of eggs], and juveniles [fry/smolts]). Two spatial entities in the program (reaches and cells) represent habitat. Reaches are longer stretches of the river and have a single daily temperature, daily turbidity, and constant food availability. Each reach is divided into cells. Each cell has its own daily velocity, daily depth, constant percent cover, and constant percent gravel. Cells get their velocity and depth value through lookup tables which list the depth and velocity of each cell for a specific flow. Adults enter a specified reach and decide when and in what cell to spawn. They then guard their redd until death. The eggs in the redd develop at a temperature-dependent rate. During incubation, eggs can experience mortality from high/low temperature, scour, dewatering, or superimposition (a female salmon making a redd on top of an existing redd). After juveniles emerge, they begin feeding and growing. They feed by catching drift food. Turbidity, water velocity, fish size, and duration of daylight all affect feeding duration and efficiency. The juveniles suffer mortality from predation, stranding, poor body condition, and temperature. Turbidity, cover, depth, temperature, duration of daylight, and juvenile size all affect the risk of predation. Each day, juveniles select a cell within a reach to inhabit based on predicted survival. Eventually, they will decide, or lack of good habitat will force them, to migrate to downstream reaches and finally out of the modeled system.

inSALMO requires several data sources and other programs to produce five types of inputs (simulation grid structure, reach level inputs, hydrologic inputs, cell level inputs, and physiology inputs). The general structure of the DST is 2D HEC-RAS simulations, and user inputs formatted with QGIS plugins are input into inSALMO (Fig. 1). Inputs for this DST include river flow, temperature, and turbidity; fish physiology; food availability; river bathymetry; available cover from flow and predation; available spawning gravel; and a grid covering the simulation area. Because this is an initial hindcast for calibration, the work flow for this paper is slightly more complicated than the basic DST (Fig. 1).

Simulation grid structure

My model domain was a 96-km portion of the Sacramento River from Keswick Dam to just past Red Bluff Diversion Dam (RBDD), which I divided into six reaches each approximately

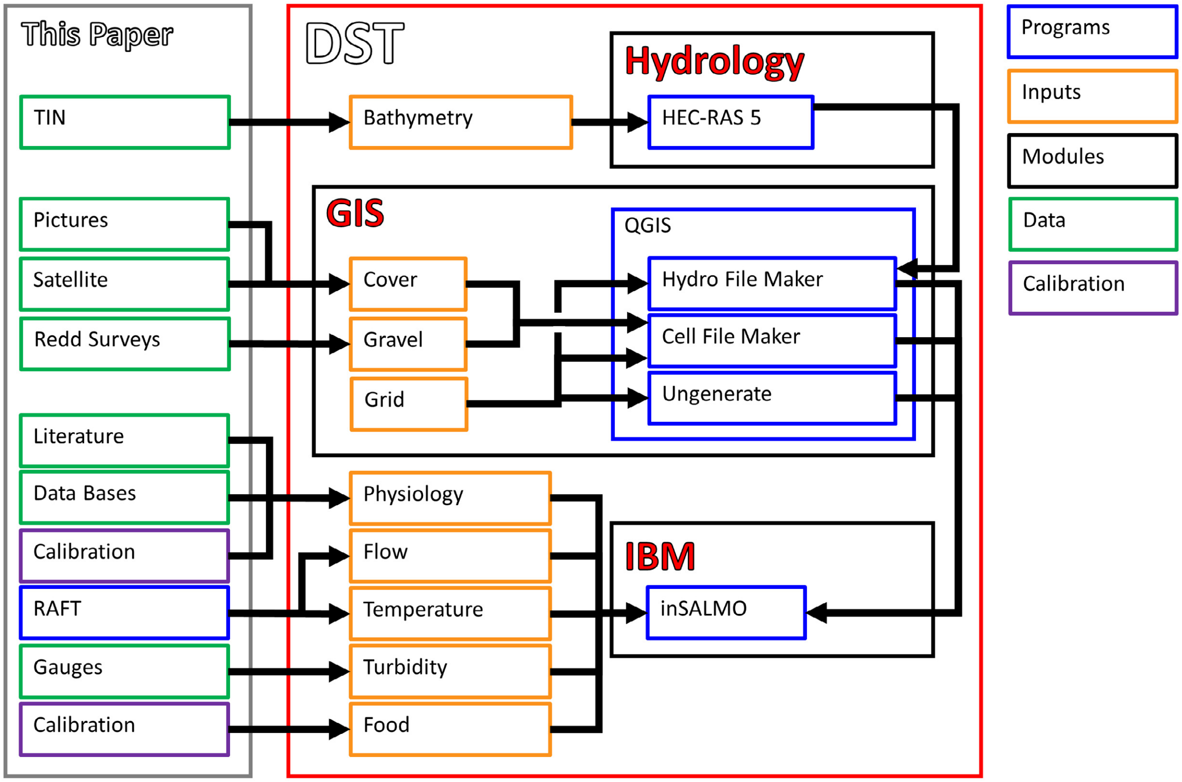

Fig. 1. A flow diagram of the model data inputs and components. The red frame outlines the decision support tool (DST). Items in the gray box are specific to this implementation of the DST.

16 km long (Fig. 2). As each reach in the model would have a single uniform temperature for each day, I chose a length that, in reality, has a small yearly average temperature difference over the extent (~0.25°C). I set the inSALMO grid size to 20 m^2 and ensured that it covered all potential wetted areas during the maximum considered flow. I selected 20 m^2 as it is small enough to allow small juveniles to explore nearby cells but large enough to provide adequate food resources to large juveniles. Our custom QGIS plugin "Ungenerate" converts the grid shape file into the format inSALMO requires (https://plugins.qgis.org/plugins/Ungenerate/).

Reach level inputs

For this implementation of the DST, reach level flow and temperature were from River Assessment for Forecasting Temperature (RAFT), a 1D hydraulic model coupled to an energy balance model operating on a 15-min time step with a 2-km spatial resolution (Appendix S1: Fig. S1; Pike et al. 2013). For this implementation of the DST, reach level turbidity came from historical gauge data from five gauges along my model domain (Station IDs: KWK, CCR, JLF, BND, and RDB; Fig. 2). These data are housed on the California Department of Water Resources (CDWR) Water Data Library. I removed gauge data that were clearly nonphysical (e.g., negative turbidity) and used interpolation to fill in gaps. Managers using this system as a DST could use any future forecasts or assumed future temperatures, flows, and turbidities.

Hydrologic inputs

Converting reach level flow into cell level depth and velocity for the above-mentioned lookup tables required river bathymetry and hydrologic modeling. For this implementation of the DST, I used a triangular irregular network (TIN) file made from CDWR and the Army Corps' Hydrologic Engineering Center's *Sacramento and San Joaquin River Basins Comprehensive Study* in 2001

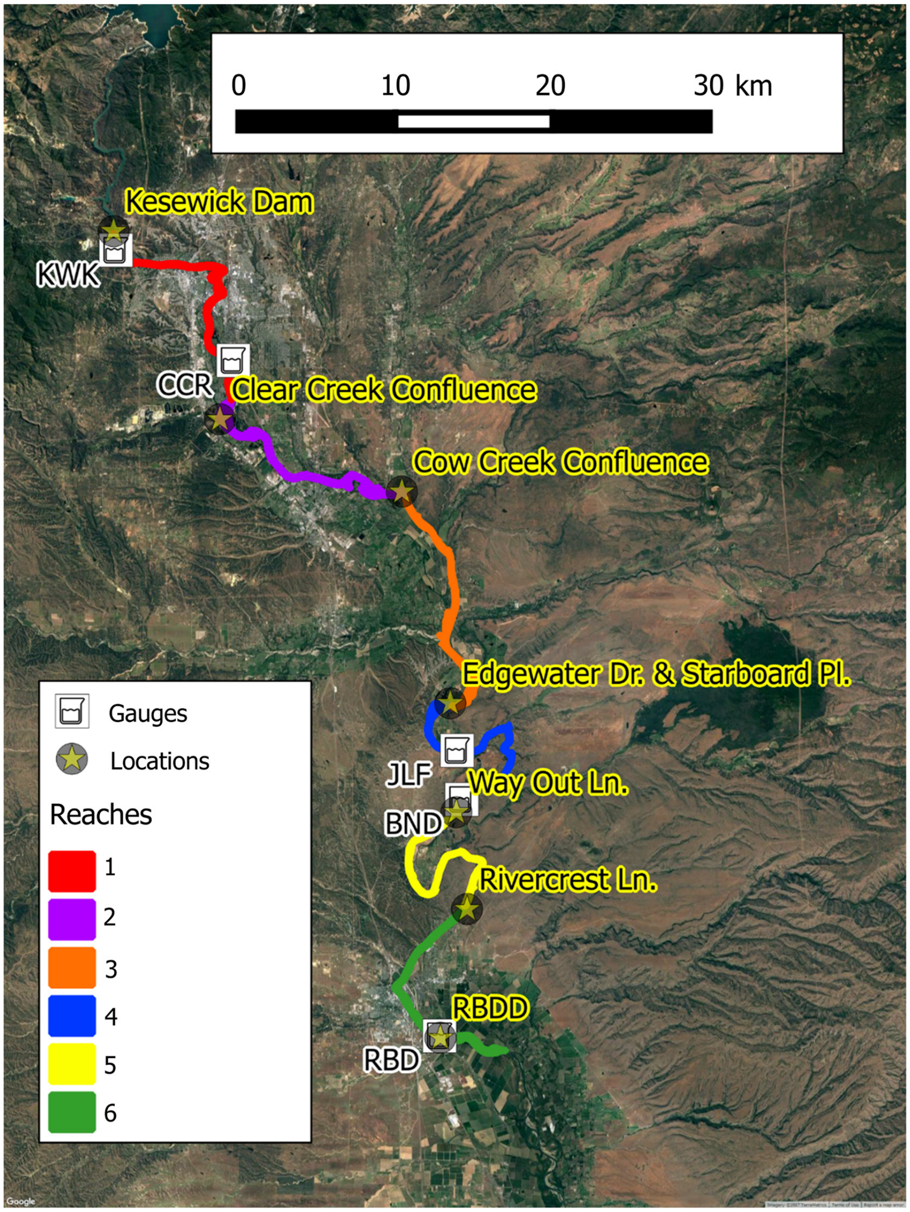

Fig. 2. All six reaches of the inSALMO run superimposed on a satellite image. Location labels divide up the six reaches. The beaker icons mark the locations of the turbidity gauges (KWK, CCR, JLF, BND, and RDB). All the spawning occurs in reach 1 with the majority occurring in the upper half.

(U.S. Army Corps of Engineers 2001). The river bed portion of the TIN was made by interpolating between cross-sectional surveys of the river bed, with cross spacing between 1.3 and 0.16 km depending on local morphology. I used AutoCAD Civil 3D 2016 to convert the TIN to a raster with 3.05-m resolution (Appendix S1: Fig. S2). This conversion step was only necessary given the only format our bathymetry data were available in was a TIN. Many bathymetry data sets for rivers are already in raster format and can be directly read into HEC-RAS 5. HEC-RAS 5 is also capable of making a raster from river cross-sections and bare earth rasters.

I imported this raster into HEC-RAS 5.0.3 (U.S. Army Corps of Engineers 2001) and constructed a structured simulation grid consisting of 625,335 cells with 9.15 m^2 grid size. I set the Manning's N to match a previously validated CDWR 1D HEC-RAS model and used that previous model's drawings of the Anderson Cottonwood Irrigation District Diversion Dam as the input for that structure in my simulation. I ran scenarios with flows from 56.6 to 453.1 m^3/s incrementing by 28.3 m^3/s and then 566.3–22,653 m^3/s incrementing by 566.3 m^3/s. From each simulation, I extracted both a velocity raster with 9.15-m^2 resolution and a depth raster with 3.05-m^2 resolution (Appendix S1: Fig. S3). I then used our custom QGIS plugin "HydroFileMaker" to average those rasters over the inSALMO 20-m^2 grid to make the first of two cell input files (cell velocity and depth; https://plugins.qgis.org/plugins/HydroFileMaker/; Table 1).

Cell level inputs

I used a combination of satellite imagery- and ground-based photographs to account for two forms of cover, from predation (distance to cover) and flow (percent cover). I constructed polygons around areas with consistent levels of cover and assigned each to one of three categories 10% cover, 50% cover, and 100% cover (main channel, over bank, and noticeable cover, respectively; Fig. 3). This classification resulted in a total of 80 km^2 of cover or about 65% of the model domain. To determine distance to cover, I calculated the average distance between an internal point and a specific corner for a 20-m square (~16 m) and set that to the distance to cover if the cell had zero percent cover. I then set 0 m as the distance to cover for a cell with 100% cover. This method results in the following equation to convert percent cover to distance:

$$\text{Distance to Cover (m)} = \frac{16(100 - \text{Percent Cover})}{100}$$

To determine to total spawning gravel present in the system, I used a similar approach to past Sacramento River gravel assessments (Stillwater Sciences 2007). I used the locations of winter-run redds from 1995 to 2013 surveys and assumed there was gravel for some buffer distance around each redd location. I set the buffer distance by comparing a detailed visual gravel survey of a 3.3-km portion of the upper Sacramento River with the amount of gravel various buffer distances would yield along that 3.3 km portion (North Stare Resources 2012). That amount of gravel matched for a buffer distance of 36 m (Appendix S1: Fig. S4). As many of the buffers overlap significantly, this method does not result in every redd contributing a 36 m radius circle worth of gravel. This method calculates a total of 1.1 km^2 of gravel. I then used our custom QGIS plugin "CellFileMaker" to average those three polygon layers (gravel and two types of cover) over the cells in the inSALMO 20-m^2 grid to make the second cell input file (cell habitat quality; https://plugins.qgis.org/plugins/CellFileMaker/).

Physiology inputs

Physiological and behavioral parameters came from literature and available databases (Appendix S1: Table S2). I attempted to use data from winter-run Chinook if available. If no winter-run data were available, I then attempted to use California populations of Chinook, then Chinook in general, and finally salmonids in general. I used R version 3.2.2's base package function glm to do necessary logistic or linear fitting (Appendix S1: Fig. S5). Data constrained parameters with little available data, but they were

Table 1. The work flow order and resolutions for each step of converting the initial TIN bathymetry into the inputs for the inSALMO grid.

Work Flow Step	Object	Dimensionality	Resolution	Units
1	TIN cross-sections	1	1.30–0.16	km
2	Raster	2	3.05	m^2
3	HEC-RAS grid	2	9.15	m^2
4a	Depth raster	2	3.05	m^2
4b	Velocity raster	2	9.15	m^2
5	inSALMO grid	2	20	m^2

Note: TIN, triangular irregular network.

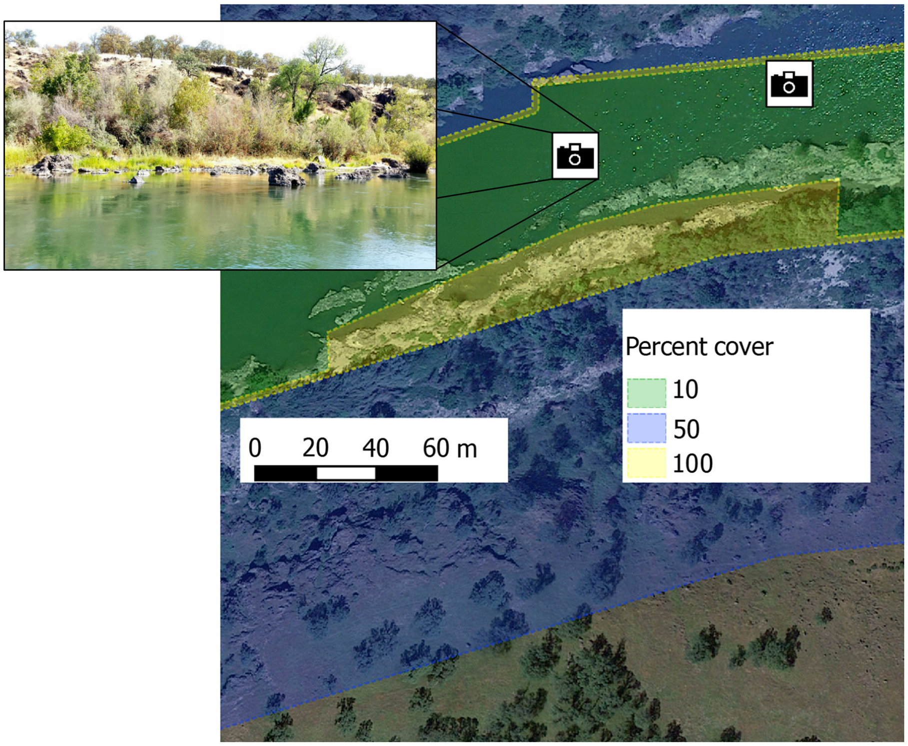

Fig. 3. An image of the percent cover polygons overlaid on a satellite image. Camera icons are locations of geolocated photographs. The percent cover polygons contour to the flow simulation boundary and therefore do not contour precisely to the river bank in the satellite image.

not statistically fitted (Appendix S1: Fig. S6). I used this method for four parameters (max move distance, and the effects of turbidity, size, and temperature on predation). For some parameter values with complex shapes (e.g., C_{max} vs. temperature), inSALMO uses a set of control points and linear interpolation to find values for set conditions. I chose control points for these parameters in an attempt to capture important aspects of the functions shape (Appendix S1: Fig. S7).

As I am attempting to match historical data, past population numbers are also necessary. I used population data from the U.S. Fish and Wildlife Service including number of spawners, fraction of females, arrival times, and fork lengths (FLs) for adults and counts, FLs, and timing of migration past RBDD for juveniles (Appendix S1: Table S1). The adult population data are carcass counts, and therefore, I assumed redd production happened 10 d before a carcass was found.

There were four parameters in the program for which I did not have any data (the concentration of food [habDriftCon], the rate at which drift food regenerates [habDriftRegenDist], and the size at which juveniles think it safe to migrate downstream [fishOutmigrateSuccessL1 and fishOutmigrateSuccessL9]). I set these parameters by using the even years of the 18 yr of field data as calibration runs and adjusted these parameters to get the best fit of the inSALMO program to field data. I first adjusted fishOutmigrateSuccessL1 and fishOutmigrateSuccessL9 to get fish of adequate size coming out late in the season. I then changed the two food parameters to get lowest average absolute percent error for both FL and population estimates passing RBDD. I then used the odd years as the validation data. All IBM data will be archived with Dryad upon acceptance.

To create a benchmark performance, I compared inSALMO to a simple linear model of outmigrating juveniles (outmigrants) vs. females and outmigrant FL vs. females to predict counts and FLs of outmigrants. I also constructed a GAM (using the R package mgcv 1.8-12). The best performing GAMs were as follows:

$$\frac{N_\mathrm{o}}{N_\mathrm{f}} = \mathrm{te}(t, N_\mathrm{f}) + \mathrm{te}(T, F)$$

$$L_\mathrm{o} = \mathrm{te}(t, N_\mathrm{f}) + \mathrm{te}(T, F)$$

where N_o is the number of outmigrants, N_f is the number of spawning females, t is days since spawning began, T and F are, respectively, average temperature and flow during the spawning through outmigration time period, and te is a tensor product smoother. Generalized cross-validation selected the basis dimension for both splines. I did a similar calibration/validation procedure with these models.

I conducted a sensitivity analysis by changing the various parameters, or parameter sets, by 10% to determine the effect on outmigration count and average FL.

Finally, I examined outputs from inSALMO that would be relevant to managers. I looked at both yearly and daily time steps. Using a Bayesian framework with non-committal priors, I analyzed correlations between many ecological drivers and superimposition, predation, age at outmigration, stranding risk, length at outmigration, and number of fish in different size classes. I present some of the interesting findings.

RESULTS

The calibration results for outmigrant counts showed generally good agreement, with the exception of two years with over 50% percent error (2010 and 2014; Fig. 4). For FL, there was a very small range in the data, but the calibration also showed good agreement with the highest percent error of 14.6% in 2014 (Fig. 5). The calibration showed fair agreement with the timing of the outmigration. inSALMO agreed with field data well for some years and did have large juveniles on the distribution's tail, but in general, inSALMO's timing of outmigration was more peaked than field data (Fig. 6).

The validation results showed fair agreement in outmigrant counts with 1997, 2011, and 2015 showing over 50% percent error (Fig. 4). I conducted multiple inSALMO runs with different random number generator kernels, which produced low variability in the program indicating that it is stable to random effects. There was generally fair agreement with FL with a maximum error of 30.0% in 1999 (Fig. 5), while outmigration timing shows similar results to the calibration runs (Fig. 6).

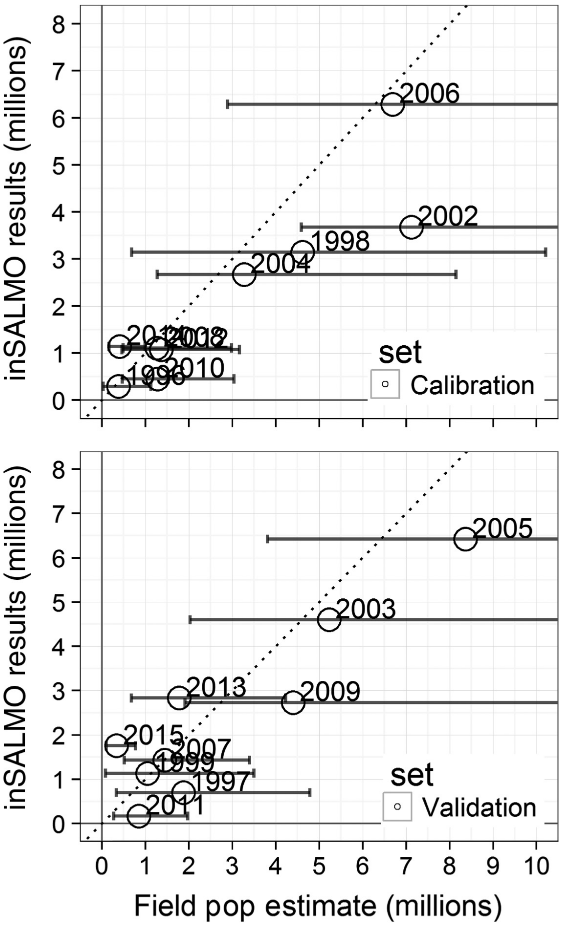

Fig. 4. Plot comparing the size of the outmigrant population calculated from inSALMO vs. the population measured in the field for all years (from 1995 to 2013 excluding 2000 and 2001 when there were no field data). Upper graph is calibration years and lower graph is validation years. Error bars are 90% CI of field estimates. The dotted line is a 1:1 line.

In comparison, both the GAM and linear model performed well for population estimates (Appendix S1: Figs. S8, S9), and fair for FL (Appendix S1: Figs. S10, S11). The linear model estimated a similar FL for each year, and the

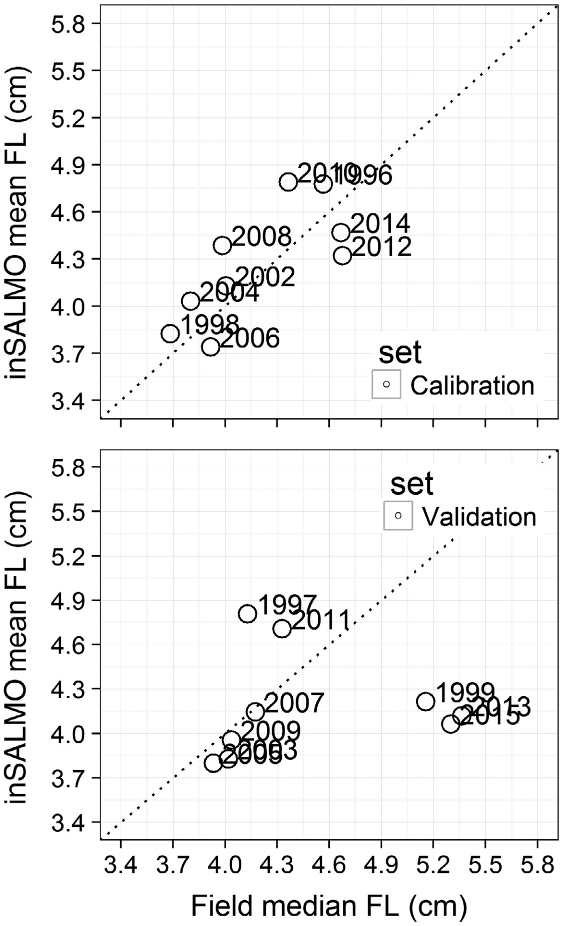

Fig. 5. Plot comparing the fork lengths (FLs) of the outmigrant population calculated from inSALMO vs. the FLs measured in the field for all years (from 1995 to 2007 excluding 2000 and 2001 when there were no field data). Upper graph is calibration years and lower graph is validation years. The recorded measures are mean for inSALMO and median for field data. Comparison between mean and median for a subsample where raw data were available showed no significant difference between the two measures. The dotted line is a 1:1 line.

GAM did excellent in FL calibration but poor in validation. Comparing the average absolute error for all years of all three, inSALMO compares well to the GAM and linear model when considering medium error in population counts. inSALMO does have a higher mean error in population counts owing to outliers (2014 and 2015). inSALMO also compares well when considering FL. The linear model performs the best for FL while poor validation performance hurts the GAM (Figs. 7, 8).

The sensitivity analysis showed overall the program was stable (Appendix S1: Table S3). Changing the fecundity parameters resulted in large effects on the outmigrant counts, and a smaller but appreciable effect from changing some parameters related to energy intake and use (e.g., fishSearchArea, fishRespParamA-D, mortFishConditionK1 and 9, and fishMaxSwimParamA-C) and some related to decisions about future fitness (e.g., fishFitnessHorizon, fishOutmigrateSuccessL1 and 9). For FL, the most sensitive parameters were related to the effect of water velocity during spawning (fishSpawnVSuitS1-6 and fishSpawnVSuitV1-6), turbidity when feeding (fishTurbidExp and Threshold), and depth under predation threat (mortFishAqPredD1 and 9).

inSALMO showed that on an annual total basis, there is a significant correlation between the rate of superimposition and the total number of eggs in the system (Fig. 9). Superimposition overwhelms the effect of temperature-induced mortality. Explicitly, temperature does not have a significant effect of the fraction of fry emerged vs. viable eggs laid unless the eggs killed by superimposition are removed from the count of viable eggs laid. On a daily basis, the risk of predation rapidly increases and begins to taper off at 50,000 juveniles and approaches a maximum of about 25% (Fig. 10). Decision support tool results indicate that turbidity provides relief from predation during juvenile migration (Fig. 10) and annual observed data confirm this effect (Fig. 11). Unlike turbidity, annual data did not show any relation between the fraction of juveniles that successfully outmigrate and the temperatures or flows they experience. In inSALMO, there is set predation pressure and limited predation cover, so as the number of juveniles increases, one might expect the fraction predated to increase. Counterintuitively, on an annual basis, there was no significant relationship between the total number of fry that emerged and the fraction that were predated (Fig. 12); however, the majority of creditable slopes were negative. The modeled residence time of the fish in the systems explained this result. As the number of fry emerged increased, the average amount of time juveniles spend in

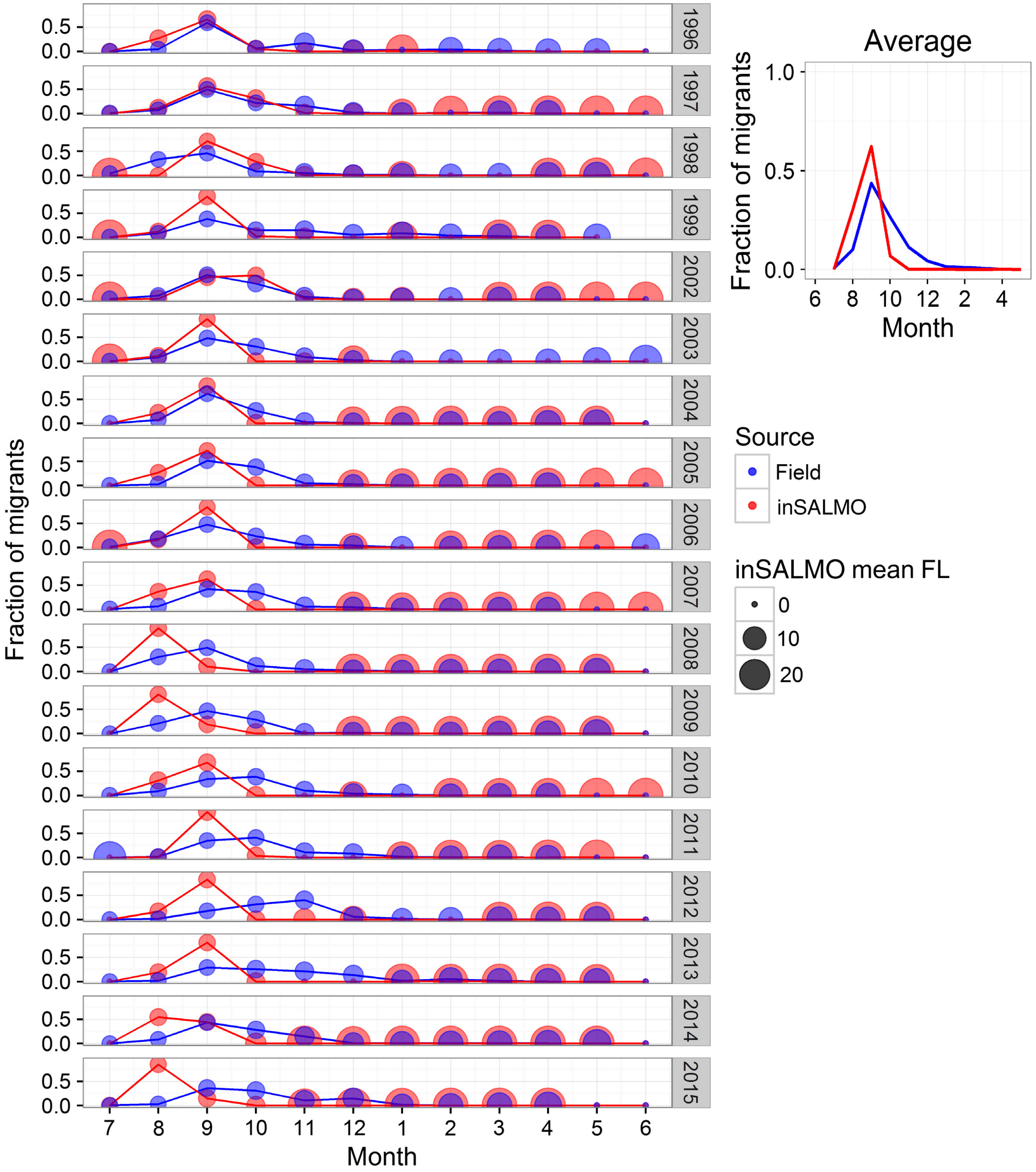

Fig. 6. The monthly distribution of outmigrants from the calibration runs (data marker area represents fork length). Generally, inSALMO has a more peaked distribution than the field distributions which can be seen in the average across all years in the lower right inset. Both data sets have long tails where the larger salmon outmigrate.

the system decreased, and as a result, they are exposed to predation for less time (Fig. 13). At the daily time scale, the risk of juveniles stranding did increase as flows decreased; however, this effect was not apparent when looking at an average annual scale (Fig. 14). As the total number of fry that emerged increased, the average size at outmigration decreased (Fig. 15); in

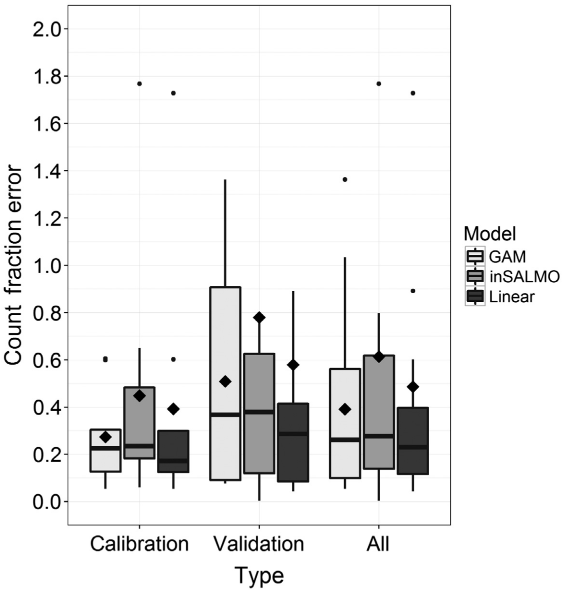

Fig. 7. Box plot (with diamonds marking the means) comparing the percent error in outmigrants for the three types of model across three different groupings. Looking at the errors in the all years grouping, inSALMO performs best.

addition, the total number of outmigrants that are large (>5 cm) and that are very large (>8 cm) increased significantly as the number of fry increased (Fig. 16; Appendix S1: Fig. S12). In other words, as the count climbs, the fraction of small fish increases faster than the large fish and reduces the average FL.

Discussion

Dams, diversions, landscape modifications, and reservoir operations have fundamentally altered many large rivers and their associated fish communities. Managers need tools to evaluate the impacts of water operations and habitat actions on the downstream communities. I successfully applied the IBM inSALMO and linked it with two other programs to model outmigrating winter-run Chinook salmon population characteristics from the study portion of the upper Sacramento River. This effort shows that these three free, GUI-based programs and my custom, publically available plugins form a useful DST for managers on large regulated rivers with resident salmonid populations.

inSALMO demonstrated several advantages over the more flexible GAM approach: (1) inSALMO median percent error was lower, (2) inSALMO allowed much more experimentation with ecological inputs, and (3) inSALMO provided more detailed outputs. The large number of ecological inputs means inSALMO could evaluate a wide variety of management actions (from gravel augmentation to flow management). The more detailed outputs can present a more complete picture of an observed phenomenon, for example, showing that reduced juvenile residence time causes reduced predation at higher numbers of juveniles. The detail of the outputs also allows managers to analyze the salmon population in different ways. For example, the DST outputs indicate that there is no relationship between outmigrants over 5 cm and the total number of fry emerged, which might indicate that the number of large outmigrants is limited by quality rearing area above RBDD. An additional benefit of inSALMO is the physiological nature of many of its parameters, which allows modelers to quickly account for new estimates of

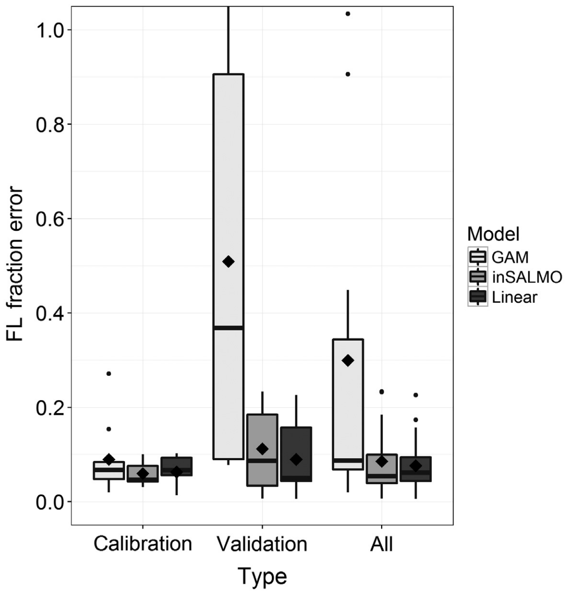

Fig. 8. A box plot (with diamonds marking the means) comparing the percent error in fork length (FL) for the three types of model across three different groupings. Looking at the errors in the all years grouping, inSALMO performs second best behind the basic linear model.

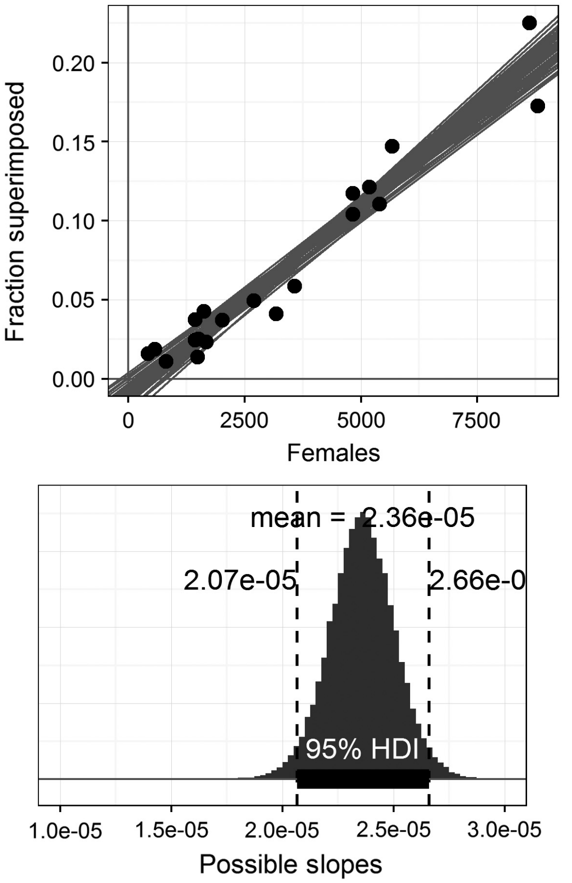

Fig. 9. A Bayesian linear regression of the annual rate of superimposition (superimposition per viable egg) vs. total eggs. The top frame shows the data superimposed over a subsample of probable regression lines. The bottom frame displays the posterior distribution of probable slopes. Zero is not inside the 95% high-density interval (95% HDI) of the posterior distribution, and thus, the relationship is significant.

these parameters from the literature as they become available (e.g., recent indications that Chinook salmon eggs may be more sensitive to high temperature than previously indicated; Martin et al. 2016).

The 18-yr inSALMO analysis generated some valuable management-related results for the study portion of the Sacramento River. Superimposition and predation were the leading causes of mortality, turbidity helped reduce predation, and carrying capacity for large juveniles was reached frequently during the study period. The contrast between the daily vs. annual observed effect of flow on stranding highlights the importance of inSALMO's ability to analyze finer temporal scale (daily) data. Throughout the year, flow varies enough on a daily basis to obscure its effect on stranding on an annual basis, but the daily analysis shows that the risk of stranding does increase as the flow is decreased. Simulations also indicate habitat limitation for rearing juveniles: Daily predation risk per individual increased quickly as juvenile abundance increased (Fig. 11), age of the outmigrants declined with total number of fry emerged, and the constant number of large outmigrants (FL >5 cm) with increasing total fry emerged. However, food limitation may also explain the latter two phenomena. There was only a single partial gravel survey of the spawning area available as input data, and therefore, these historical inSALMO runs cannot elucidate how adding gravel area or placing gravel in new locations might affect the superimposition risk. Future inSALMO runs could not only simulate the most effective amount of gravel to add, but also the

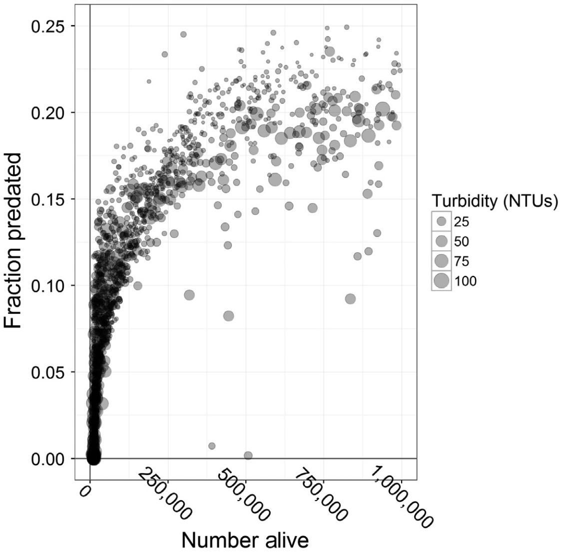

Fig. 10. A scatter plot of the daily fraction of fish predation kills vs. the number alive that day. Each data mark is sized to represent the daily turbidity level. The mark is partially transparent to help show where there is high clustering of data points. The *x*-axis is divided to clearly show a region with little increased predation as the number of fish increase and a region with increased predation as the number of fish increase. This transition happens at around 500,000 fish.

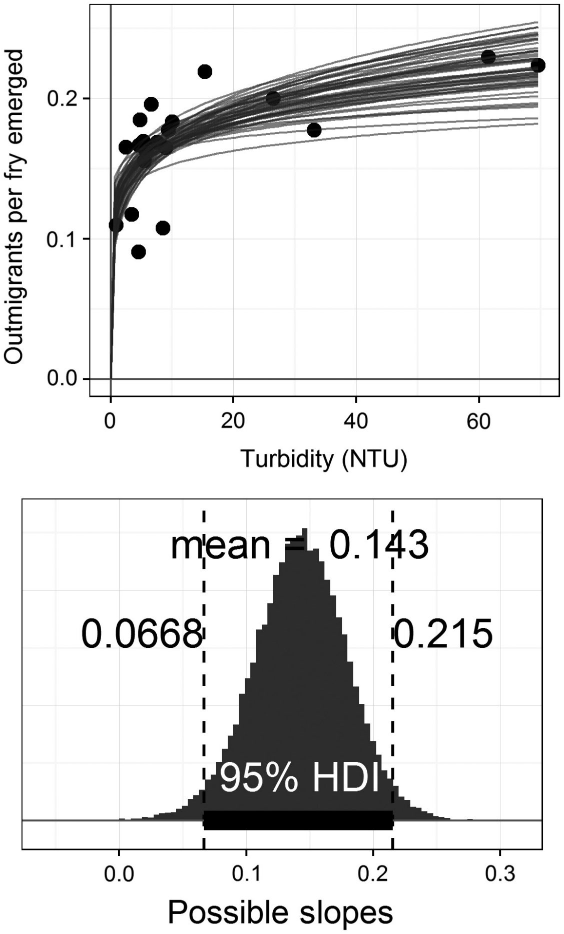

Fig. 11. A Bayesian power regression of the annual fraction of successful outmigrants (outmigrants per fry emerged) vs. average turbidity a fish experienced. The top frame shows the data superimposed over a subsample of probable regression lines. The bottom frame displays the posterior distribution of probable slopes. Zero is not inside the 95% high-density interval (95% HDI) of the posterior distribution, and thus, the relationship is significant.

optimal locations, which may affect the gravel supplementation success.

These hindcasts provide examples of the rich data sets and analyses that managers could use to help make management decisions. Managers could use information about superimposition risk (Fig. 9) to assess the effectivity of gravel augmentation, simply by expanding the gravel polygons in QGIS and using the "CellFileMaker" plugin to produce a new cell input file (Fig. 1). On a daily time step, managers could use the modeled predation relationships (Fig. 10) to assess the usefulness of adding cover such as root balls or large woody debris to the river. Similar to the spawning gravel test, managers could expand the area of the cover polygons, add new cover polygons, or increase the fraction of cover each polygon represents in QGIS and use the "CellFileMaker" plugin to produce a new cell input file (Fig. 1). When considering different water release scenarios, managers could consult the relationships on various effects of flow and

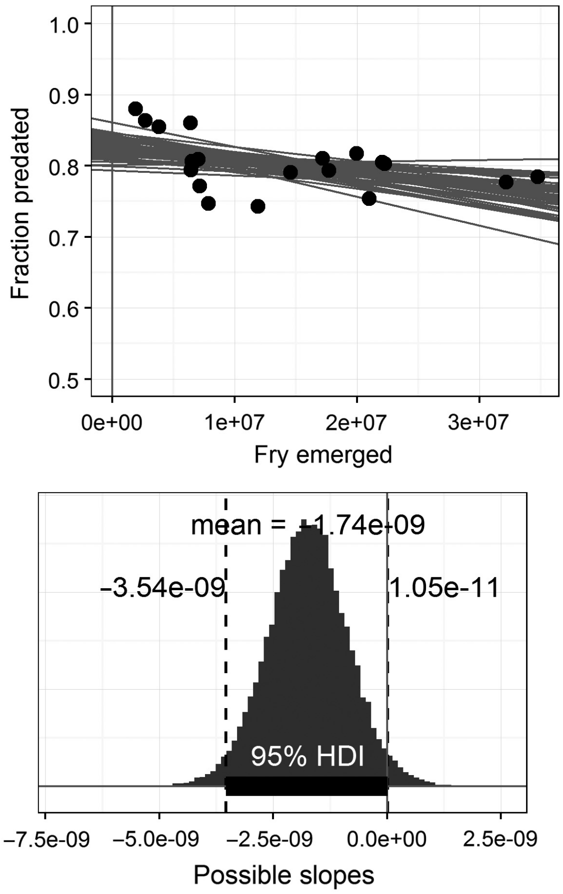

Fig. 12. A Bayesian linear regression of the annual predation rate (predation per fry emerged) vs. fry emerged from redds. The top frame shows the data superimposed over a subsample of probable regression lines. The bottom frame displays the posterior distribution of probable slopes. Zero is inside the 95% high-density interval (95% HDI) of the posterior distribution, and thus, the relationship is not significant.

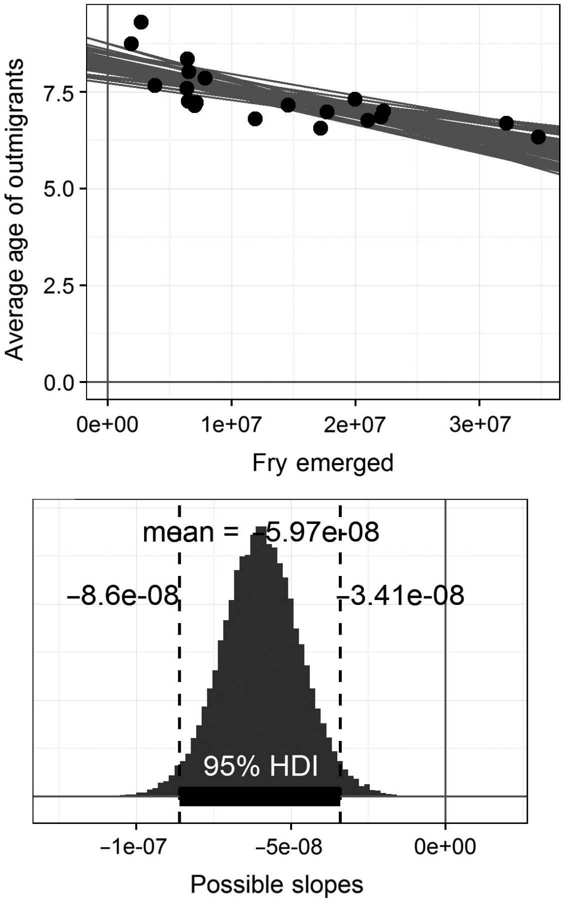

Fig. 13. A Bayesian linear regression of the annual average age at outmigration vs. fry emerged from redds. The top frame shows the data superimposed over a subsample of probable regression lines. The bottom frame displays the posterior distribution of probable slopes. Zero is not inside the 95% high-density interval (95% HDI) of the posterior distribution, and thus, the relationship is significant.

turbidity (Figs. 11, 14) to assess the potential dangers/benefits. Conducting tests of this type is a simple matter of changing a flow and turbidity input files in any spread sheet program (Fig. 1).

inSALMO can help answer important questions about the effects of anthropogenic climate change, flow management, and habitat restoration actions on the spawner through smolt portions of the Chinook salmon life cycle. Future applications using this implementation of inSALMO will vary one input while holding all the others constant to evaluate the effects of various abiotic factors. Modeling experiments of this next type could answer important management questions such as “Are the number or large juveniles in the system limited by habitat?” and “Will providing more cover have an effect on the population, FL, or both?” inSALMO’s ability to track individual fish allows users to not only learn how a potential action will affect a population as a whole, but also how it will affect each life stage. This capability is important as restoration actions may have beneficial effects on one

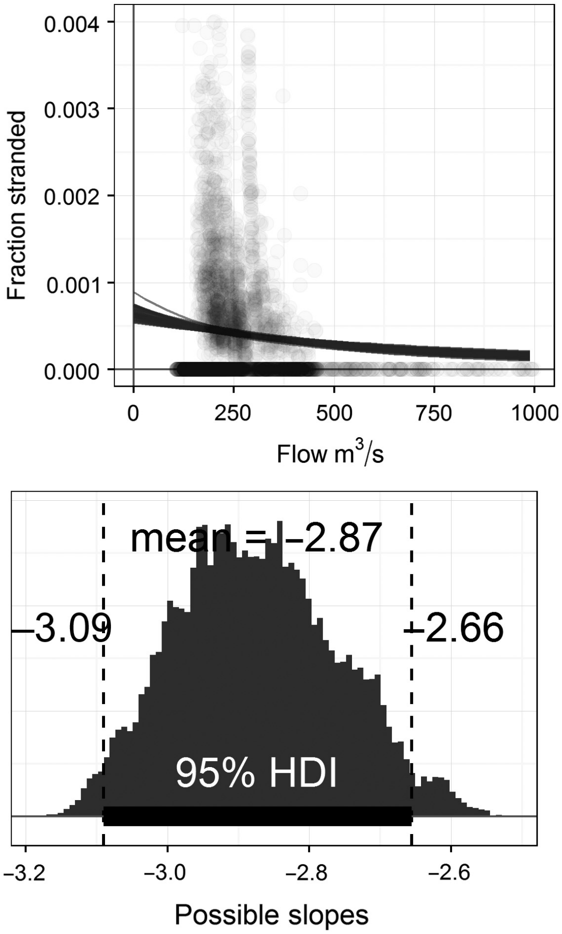

Fig. 14. A Bayesian power regression of the daily stranding rate (stranding per fry in the system) vs. flow. The top frame shows the data superimposed over a subsample of probable regression curves. The bottom frame displays the posterior distribution of probable slopes. Zero is not inside the 95% high-density interval (95% HDI) of the posterior distribution, and thus, the relationship is significant.

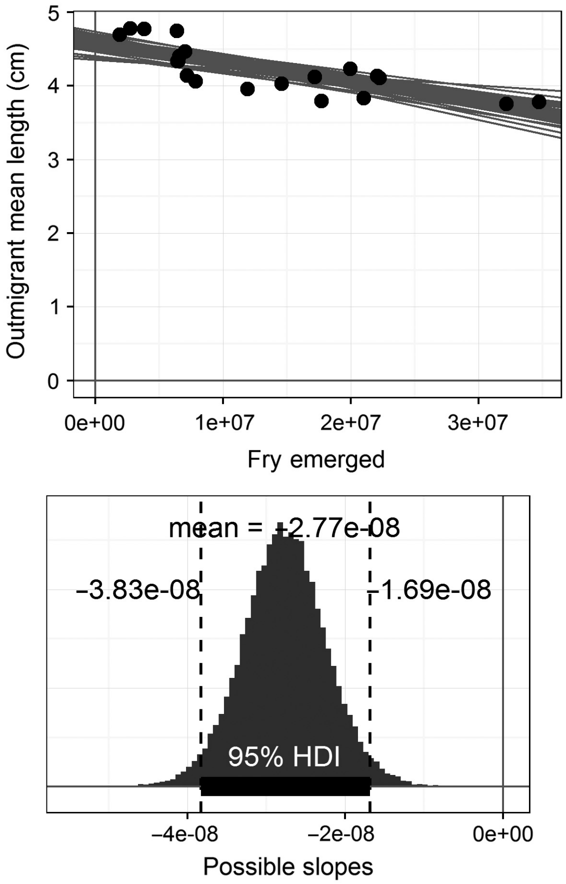

Fig. 15. A Bayesian linear regression of the annual mean fork length vs. number of fry emerged. The top frame shows the data superimposed over a subsample of probable regression curves. The bottom frame displays the posterior distribution of probable slopes. Zero is inside the 95% high-density interval (95% HDI) of the posterior distribution, and thus, the relationship is not significant.

life stage and detrimental on another (Railsback et al. 2013). Thus, I see promise for using this DST to assess potential effects of habitat restoration, water management scenarios, and increasing temperatures on fish stocks and life stages. For example, resources are limited for gravel additions or side channel restoration; inSALMO could inform managers on how best to divide these resources. In addition, inSALMO could help determine productive restoration locations and then evaluate what effects these actions might have under anthropogenic climate change.

There are areas where inSALMO could improve, such as in the accuracy of predicting the temporal spread of the outmigrants and the population counts in the drought years 2014 and 2015. With respect to migration timing, I was unable to find a consistent pattern among years when inSALMO performed poorly, and thus, further investigation of why some years have poor matches is needed. The poor fits in 2014 and 2015 are most likely due to some phenomena that occurred during these two critical drought

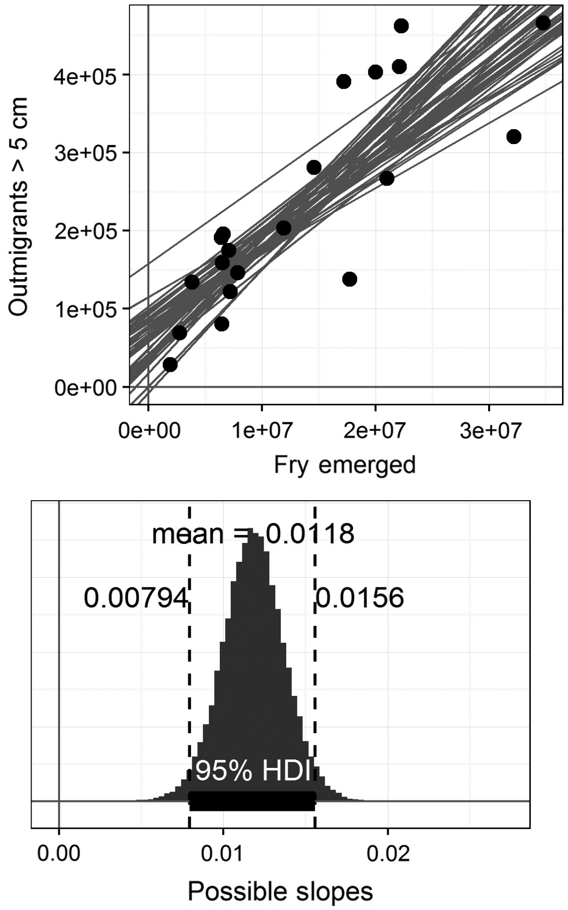

Fig. 16. A Bayesian linear regression of the annual fraction of salmon over 5 cm vs. the total number in the system. The top frame shows the data superimposed over a subsample of probable regression curves. The bottom frame displays the posterior distribution of probable slopes. Zero is outside the 95% high-density interval (95% HDI) of the posterior distribution, and thus, the relationship is significant.

years which inSALMO is either not considering (temperature dependence on available food, siltation of redds due to low flows, etc.) or is modeling poorly. Using IBMs as potential DSTs does pose some problems. They are computationally intensive to run; if attempting to account for many phenomena, they require substantial amounts of input data, and if not including enough or including the wrong phenomena, they could potentially misattribute the driver of a result. Thus, before model construction, modelers must make assumptions which phenomena likely have a significant effect on the system and how to incorporate them. Fulfilling this requirement can make model construction quite time-intensive.

inSALMO's spatially explicit nature and the number phenomena it includes make it a particularly useful tool for evaluating habitat restoration, and, I would argue, more suitable than most current population modeling approaches. I think that the ability of inSALMO-type models, when paired with all GUI-based supplementary programs, to independently account for many ecological drivers and the fullness of the data they produce make them good potential candidates for a DST on regulated rivers.

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LITERATURE CITED

Bates, P., J. Chandler, K. Lepla, and K. Steinhorst. 2014. Using mark-recapture data in an individual-based model to evaluate length-at-age differences between two Snake River white sturgeon (*Acipenser transmontanus* Richardson, 1836) populations in Idaho, USA. Journal of Applied Ichthyology 30: 1319–1327.

Crozier, L., and R. W. Zabel. 2006. Climate impacts at multiple scales: evidence for differential population responses in juvenile Chinook salmon. Journal of Animal Ecology 75:1100–1109.

DeAngelis, D. L., and V. Grimm. 2014. Individual-based models in ecology after four decades. F1000Prime Reports 6:39.

Dynesius, M., and C. Nilsson. 1994. Fragmentation and flow regulation of river systems in the northern 3rd of the world. Science 266:753–762.

Hydrologic Engineering Center. 2016. Hydrologic Engineering Center's river analysis system. Hydrologic Engineering Center, Davis, California, USA.

Katz, J., P. B. Moyle, R. M. Quiñones, J. Israel, and S. Purdy. 2013. Impending extinction of salmon, steelhead, and trout (*Salmonidae*) in California. Environmental Biology of Fishes 96:1169–1186.

Krause, C. W., T. J. Newcomb, and D. J. Orth. 2005. Thermal habitat assessment of alternative flow scenarios in a tailwater fishery. River Research and Applications 21:581–593.

Mantua, N., I. Tohver, and A. Hamlet. 2010. Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. Climatic Change 102:187–223.

Martin, B. T., A. Pike, S. N. John, N. Hamda, J. Roberts, S. T. Lindley, and E. M. Danner. 2016. Phenomenological vs. biophysical models of thermal stress in aquatic eggs. Ecology Letters 20:50–59.

McDermot, D., and K. A. Rose. 2000. An individual-based model of lake fish communities: application to piscivore stocking in Lake Mendota. Page Ecological Modelling 125:67–102.

NOAA. 2010. Land area affected by Endangered Species Act listings of Salmon & Steelhead. NOAA, Washington, D.C., USA.

North Stare Resources. 2012. Sacramento River spawning gravel restoration and monitoring program. North Stare Resources, Redding, California, USA.

Petersen, J. H., and D. L. DeAngelis. 2000. Dynamics of prey moving through a predator field: a model of migrating juvenile salmon. Mathematical Biosciences 165:97–114.

Pike, A., E. Danner, D. Boughton, F. Melton, R. Nemani, B. Rajagopalan, and S. Lindley. 2013. Forecasting river temperatures in real time using a stochastic dynamics approach. Water Resources Research 49:5168–5182.

QGIS Development Team. 2016. QGIS Geographic Information System. Open Source Geospatial Foundation Project, Beaverton, Oregon, USA.

Railsback, S. F., M. Gard, B. C. Harvey, J. L. White, and J. K. H. Zimmerman. 2013. Contrast of degraded and restored stream habitat using an individual-based salmon model. North American Journal of Fisheries Management 33:384–399.

Reed, T. E., D. E. Schindler, M. J. Hague, D. A. Patterson, E. Meir, R. S. Waples, and S. G. Hinch. 2011. Time to evolve? Potential evolutionary responses of fraser river sockeye salmon to climate change and effects on persistence PLoS ONE 6:e20380.

Stillwater Sciences. 2007. Sacramento River Ecological Flow Study: Gravel Study Final Report. Stillwater Sciences, Berkeley, California, USA.

Sullivan, T. 2002. Evaluating environmental decision support tools. Brookhaven National Laboratory, Upton, New York, USA.

U.S. Army Corps of Engineers. 2001. HEC-HMS for the Sacramento and San Joaquin river basins comprehensive study. Pages 1–240. U.S. Army Corps of Engineers, Sacramento, California, USA.

Zeug, S. C., K. Sellheim, C. Watry, B. Rook, J. Hannon, J. Zimmerman, D. Cox, and J. Merz. 2013. Gravel augmentation increases spawning utilization by anadromous salmonids: a case study from California, USA. River Research and Applications 30:707–718.

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