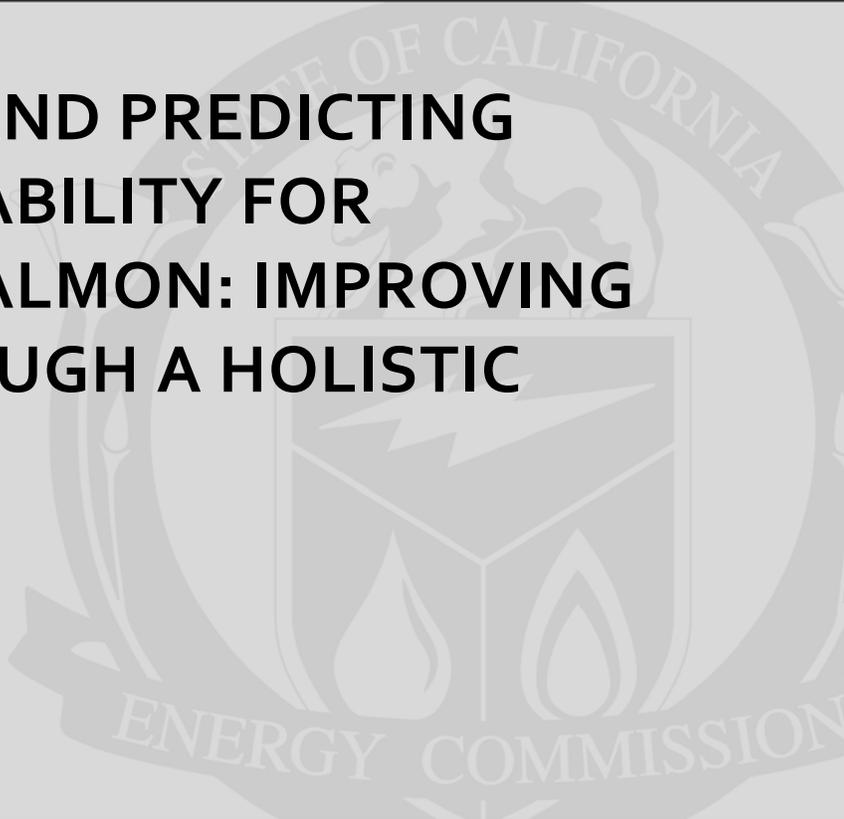


**Energy Research and Development Division  
FINAL PROJECT REPORT**

**EVALUATING AND PREDICTING  
HABITAT SUITABILITY FOR  
CALIFORNIA SALMON: IMPROVING  
MODELS THROUGH A HOLISTIC  
PERSPECTIVE**



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## PREFACE

The California Energy Commission Energy Research and Development Division supports public interest energy research and development that will help improve the quality of life in California by bringing environmentally safe, affordable, and reliable energy services and products to the marketplace.

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## ABSTRACT

The impoundment and diversion of water for hydropower generation and other purposes in many of the rivers in California's Central Valley has altered flow patterns in these rivers, often causing dramatic alterations in the amount, timing and frequency of flows. These altered flow patterns also affect the amount of habitat available for many fish species. The relationship between water flows and the quality and quantity of suitable habitat for species such as juvenile steelhead and Chinook salmon is an important element of hydropower relicensing and water allocation and can be modeled to predict the consequences of different flow regimes on species and life stages. Such modeling efforts allow managers to better evaluate flow allocations. The modeled relationships must have high predictive ability and be robust across a variety of flow-release scenarios if they are to be useful in the flow-allocation decision process. This study examined patterns of habitat projections across a series of contrasting habitat models in two California Central Valley rivers, the American and the Mokelumne. Model formulations that included different elements of salmon habitat had significantly different predictive results across different flows. This confirmed previous work that highlighted the sensitivity of these models. A bioenergetics-based habitat model was developed to establish a reliable expression of flow-habitat relationships. The flow-habitat relationship model predicted the net energy gain of a fish, the given prey density, temperature, and water velocity. This project improved the range of tools available for evaluating the influence of various regulated flow regimes on growth potential and habitat availability for threatened and endangered fish species.

**Keywords:** Salmonids, bioenergetics, water allocation impacts, hydrodynamic models, habitat suitability criteria

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# EXECUTIVE SUMMARY

## Introduction

The seasonal pattern of water discharge of a river drives geologic and ecologic dynamics. Flows can drive channel migration, sediment movement, and change the biotic communities of these systems. One of the major global alterations of river systems has been the construction of dams. Dams fundamentally change the flow pattern of downstream rivers. Sediments that would otherwise be transported downstream sink to the bottom of reservoirs and wood is trapped. Rivers downstream of dams are often depleted of sediments and large woody debris.

Pacific salmon have evolved in these dynamic river systems. Research has shown that different Chinook salmon life-histories corresponded to different hydrologic regimes. Understanding the interplay between salmon and flow regimes is critical to their management and conservation. Pacific salmon populations have declined dramatically throughout much of their southern range over the last century or so. Impassable dams have removed the majority of historic salmon habitat in the Central Valley of California. In locations such as this, salmon management strategies are confronted by economic and political realities. These systems have highly variable flow regimes, which are manipulated seasonally. Water is allocated throughout the year by trying to assess trade-offs between user groups such as water used for agriculture versus providing flows conducive to salmon spawning.

The challenges in managing and restoring salmon have inspired numerous quantitative advances such as two dimensional habitat models. These models can be applied to identify suitable habitat for salmonids and examine how suitable habitat varies across different flow regimes. Salmonids refers to the family Salmonidae, which includes salmon, trout, and whitefish. Alternatively, these models can examine how a given management action such as channel modification has altered suitable habitats for salmonids. These models connect a hydrodynamic flow model with a habitat suitability model. The habitat suitability model quantifies the characteristics of habitat that contain the target species, compared with characteristics of habitat that does not contain the target species. The habitat suitability model then applies these relationships to the hydraulic model of the targeted area to identify the location and quantity of habitat that is predicted to be suitable.

## Project Purpose

The primary objective of this project was to produce a set of habitat projections using a two-dimensional hydrodynamic model called River2D across different model formulations, and to examine patterns of these projections under different flow releases for two dam-regulated rivers in California, the American and the Mokelumne. River2D is a two-dimensional model that was customized for fish habitat evaluation studies. This project used River2D to correlate composite suitability indices with a hydraulic model to estimate weighted usable area for a species and life-stage. Weighted usable area is an index that combines elements of habitat quantity and habitat quality. For this study, rearing habitat for juvenile Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*O. mykiss*) were modeled. The researchers anticipated that these efforts would help improve the application of these modeling tools under contrasting conditions.

This project focused on three central objectives:

1. Creating models of suitable habitat across a range of flows for juvenile salmon using River2D and habitat suitability criteria provided in published literature focused on California rivers. Habitat projections from these primary models were compared against others that incorporated alternative habitat suitability criteria.
2. Generating four contrasting River2D models that included habitat suitability criteria developed from data collected at each study reach via logistic regression, habitat suitability criteria where velocity preference was bioenergetics-based and modeled as positive net energy gain (incorporating prey availability, swimming costs, fish size and water temperature) and both site-specific and literature-derived habitat suitability criteria.
3. Confronting contrasting models with data. These data consisted of large-scale snorkel surveys as well as fish sampling across available habitat types (pool, riffle, backwater, and so forth) in both study systems. Akaike information criterion (AIC) was used to determine which set and combination of habitat suitability criteria most parsimoniously described the variation in the observed data as well as assessed the relative importance of including water temperature in these models. AIC is a measure of the relative goodness of fit of a statistical model. This model comparison identified those models offering the best predictive ability across differing criteria. The principle of parsimony in this context refers to choosing a hypothesis with the fewest assumptions.

## Project Results

The researchers examined the hydraulic model produced with River 2D for hydraulic anomalies and unrealistic conditions and for differences in both measured inflow and modeled outflow. Hydraulic anomalies comprised less than one percent of the modeled reach by area, and the measured inflow and predicted outflow were within one percent of each other. The quality assurance/quality control procedures proposed by Steffler and Blackburn (2002) were used to assure that the hydraulic models were reasonable across the modeled discharges. The same hydraulic model was used for all contrasting hydrodynamic habitat models to eliminate model comparison bias.

Habitat suitability criteria were acquired from literature that focused on rivers in California to maximize applicability to the project study sites. The literature-derived habitat suitability criteria were integrated into the River2D models to produce habitat projections across a range of flows using these habitat suitability criteria for both study rivers.

Different habitat suitability data and inputs produced fundamentally different model projections and predictions. Specifically, there were substantial differences between literature-based and observation-based habitat suitability curves. For example, the decision of whether or not to include cover or substrate often made a substantial difference in the resulting projection and prediction of location and the amount of suitable habitat. The most striking differences occurred between models that included cover compared to those that did not. These variables produced fundamentally different relationships between discharge and weighted usable area on the American River. Models that included cover exhibited an increase in weighted usable area above an intermediate discharge of 3,100 cubic feet per second (cfs). The highest discharges had approximately 20 percent more identified habitat than intermediate discharges. This pattern was fundamentally different for models that included substrate rather than cover. For these models, weighted usable area only decreased as discharge increased. One such model

predicted a decrease in weighted usable area by more than 60 percent as discharge increased. The results showed that outcomes were very sensitive to even at the most coarse scale model.

Model comparisons showed that the best model for projecting the impact of variations in habitat use on the American River included the elements of velocity, depth, adjacent velocity, and water temperature. Models were evaluated with snorkeling observations and the AIC as a metric of model parsimony. It is notable that the top five models, although very close in parsimony, all included velocity, temperature, and adjacent velocity. This was evidence that these three factors were important parameters defining habitat selection by juvenile Chinook salmon. These results were supported by past findings and other studies that described the bioenergetics basis of habitat preference for drift-feeding salmonids, such as Hill and Grossman 1993.

In this study different salmonid habitat models were applied, tested, and compared. The major conclusions included:

- Literature-based and field-based habitat suitability criteria were developed for juvenile salmonids in the study rivers. Bioenergetics-based habitat suitability criteria was also developed, which allowed incorporating water temperature and food availability, without the need for altering software currently available to resource managers.
- Different habitat suitability criteria will lead to vastly different model projections. This result supports the findings of previous research, such as that by Bovee (1994).
- The location of appropriate salmonid habitat changed at different discharges. Channel morphology will influence the relationship between discharge and suitable habitat. Analyzing the different types of habitat that are suitable at different flow regimes highlighted the dynamic nature of “what is good habitat for salmonids.”
- Using a model-selection approach allowed identifying the model that best described the data. This model-selection exercise illustrated that fish habitat is best characterized by a combination of factors. The snorkeling surveys indicated that the best models included temperature, velocity, adjacent velocity, and sometimes depth and substrate.
- While these models can be insightful, the results are extremely sensitive to the model formulation. Care should be taken to properly set model parameters to obtain the most accurate predictions.

### Benefits to California

The allocation of water resources in the Central Valley is an intrinsically difficult challenge: California’s water demands conflict with the needs of species such as Pacific salmon. The potential consequences of water releases for Pacific salmon can be quantified through the use of hydrodynamic habitat models. However, these habitat models necessitate high predictive power to effectively serve this purpose. For example, different sets of models predict that increasing water flows can either decrease or increase suitable habitat. The study showed that for the American River, the most parsimonious model included velocity, depth, adjacent velocity, and water temperature. The results of this study should encourage careful and appropriate application of these models. The results highlighted the importance of a holistic approach to river management. For example, it is critical to integrate actions such as discharge

that is controlled by dam operators and channel morphology that is being changed by enhancement actions.

# CHAPTER 1:

## Introduction

Perhaps the most important defining characteristic of a river is its flow regime (Bayley 1995). The seasonal pattern of water discharge of a river drives geologic and ecologic dynamics (Bayley 1995). Flows can drive channel migration, sediment movement, and change the biotic communities of these systems (Stanford and Ward 1993). Flow regimes drive both latitudinal and longitudinal connectivity—connecting rivers to their floodplains and to their headwaters (Ward et al. 2002). For example, high flows connect rivers to woody debris on the floodplain that can provide potentially important fish habitat (Gurnell et al. 2002). Alternatively, high water flow can move sediments from high in the watershed to depositional areas lower in the watershed. These abiotic features set the ‘habitat template’ for the organisms that live in these systems.

Pacific salmon have evolved in these dynamic river systems. Beechie et al. (2006) analyzed traits of Chinook salmon (*Oncorhynchus tshawytscha*) populations and how they covaried with hydrologic regimes in the Puget Sound area of Washington. They discovered that different Chinook salmon life-histories corresponded to different hydrologic regimes—populations in snowmelt-dominated regions generally had stream-type juveniles, spawned earlier, and had older spawners than populations from rainfall-dominated systems. Research in relatively pristine areas of Alaska has suggested that such resultant life-history diversity can contribute to the sustainability and stability of salmon populations (Hilborn et al. 2003; Schindler et al. 2010). Thus, understanding the interplay between salmon and flow regimes is critical to their management and conservation.

One of the major global alterations of river systems has been the construction of dams. The majority of large rivers now have at least one major dam on them (Nilsson et al. 2005). Through holding back flows and releasing them when desired, dams and their operators can control the seasonal pattern of how much water flows down a river and when. Dams thereby provide important services for people by reducing flooding, generating energy, and providing reliable water for human consumption and agriculture irrigation. Dams fundamentally change the flow pattern of downstream rivers. Poff et al. (2007) analyzed 186 records of long-term stream flow in the continental United States that spanned time periods before and after dam construction. Across these time series, they characterized a suite of flow variables such as the timing and magnitude of high flow events. Through changing the timing and magnitude of water discharge, dams have systematically homogenized flows. In other words, patterns of river stream discharge are becoming more similar from river to river. Furthermore, dams block both lateral and longitudinal connectivity of rivers (Ward and Stanford 1995). Sediments that would otherwise be transported downstream sink to the bottom of reservoirs and wood is trapped. Rivers downstream of dams are often depleted of sediments and large woody debris.

Pacific salmon populations have declined dramatically throughout much of their southern range over the last century or so (Nehlsen et al. 1991; Gustafson et al. 2007). Lindley et al. (2006) calculated that impassable dams have removed the majority of historic salmon habitat in the Central Valley of California. In locations such as this, salmon management strategies are confronted by economic and political realities. These systems have highly variable flow regimes, which are manipulated seasonally. Water is allocated throughout the year by trying to

assess trade-offs between user groups such as water used for agriculture versus providing flows conducive to salmon spawning.

What techniques can be attempted to restore salmon populations in these highly modified systems with high demand from multiple users? One option is to release flows to try to restore the flood-pulse “process”. For example, on the Colorado River system, dam operators have recently started experimental releases of high discharges to mimic some of the past ‘flashiness’ of the downstream Grand Canyon region. Biotic communities have rapidly responded to this change in flow regime. Cross et al. (2010) found that these experimental releases of water decrease the abundance of notoriously invasive New Zealand Mudsnails. Another option is to try to restore the “patterns” generated by past flow regimes. For example, if systems have been starved of sediments by upstream dams, gravel augmentation projects can provide sediments of sizes that are suitable for salmon spawning. Alternatively, engineering projects can change a simple channelized reach into one that is highly complex through construction of side channels and floodplains (Richards et al. 1992; Heady and Merz 2006, 2007). However, most restoration projects have little financial support for accompanied monitoring to evaluate the potential success or failure of the restoration.

These challenges in managing and restoring salmon have inspired numerous quantitative advances such as two dimensional habitat models. These models can be applied to identify suitable habitat for salmonids and examine how suitable habitat varies across different flow regimes. Alternatively, these models can examine how a given management action (such as channel modification) has altered suitable habitats for salmonids. These models connect a hydrodynamic flow model with a habitat suitability model. The habitat suitability model is built by quantifying the characteristics of habitat that contain the target species, compared with characteristics of habitat that does not contain the target species. The habitat suitability model then applies these relationships to the hydraulic model of the targeted area to identify the location and quantity of habitat that is predicted to be suitable. This study applied these approaches to an examination of Chinook salmon and steelhead trout (*Oncorhynchus mykiss*) habitat in two rivers in California.

# CHAPTER 2: Building Habitat Models

## 2.1 Introduction

This project focused on a recently enhanced section of the lower American River in Sacramento, CA (Sunrise side channel: 37° 37' 42.51" N, 121° 16' 24.27" W), and a previously enhanced reach on the Mokelumne River near Lodi, CA (day use area: 37° 13' 31.00" N, 121° 01' 55.47" W). In both cases, an existing side channel was altered to allow flow at low discharges and provide useful habitat to steelhead and Chinook salmon. The project aimed to capitalize on the availability of topography data collected prior to the enhancement efforts and riverbed modification. The existing data set was refined by adding topographic points collected post restoration; throughout the entire reach, but in higher concentration in the enhanced side channels. These data were used to parameterize a hydrodynamic habitat model (River 2D, version 0.95a) to estimate weighted usable area (WUA) at nine different flow regimes for Chinook salmon and steelhead trout at the juvenile life stage (> 50mm, < 100mm). WUA was calculated with the River 2D program at 9 flows and differences in WUA were qualitatively compared.

## 2.2 Methods

Researchers began by parameterizing a two-dimensional depth-averaged model (River 2D) of river hydrodynamics under post-enhancement conditions following the methods described in Steffler and Blackburn (2002). The consolidated topographic data was utilized as key inputs in River 2D model parameterization and substrate attributes were converted to roughness values as described by Gard (2006). The methods described in Gard (2006) and Guay (2000) were followed to develop site specific habitat suitability criteria. Specifically, large-scale snorkel surveys were conducted from February to July (2009, 2010), from 8am – 4pm, and across as many different accessible habitat types as feasible. The snorkel surveys were conducted along a linear transect from downstream to upstream and marked locations of steelhead and Chinook with flagged weights. When depth and velocity were too high to allow unaided upstream snorkeling, fixed ropes were used to aid snorkeler's upstream movement. All physical habitat characteristics (such as depth, velocity) were then measured in occupied locations and noted species and an estimate of fish size. Regardless of the number of fish at each location, each observation counted as a single data point in the habitat suitability criteria model. Along each snorkel survey transect observers measured the same suite of habitat characteristics in randomly selected unoccupied locations. Researchers analyzed the binary occupied and unoccupied locations via polynomial logistic regression in program R (R Development Core Team 2007) which produced a probability of habitat occupancy. These probability estimates were converted to suitability criteria via the methods of Gard and Guay.. However, potentially due to low numbers of spawning adults, and subsequently low densities of juveniles, direct observations of habitat use were few, relative to literature standards (<150 observations). Analysis was completed with the data available; however the number of observations can influence habitat model parameterization and projections. In addition, water temperature at the beginning and end of each snorkel survey was collected to be used in AIC model comparisons and a bioenergetics-based velocity suitability model.

Habitat suitability criteria from several sources were used to complete the habitat component of the River 2D model. Researchers used Habitat Suitability Curves from United States Fish and Wildlife Service (USFWS 1989, 1997) for juvenile steelhead. Substrate and cover suitability for both species was obtained from Instream Flow Study Guidelines (WDFW 2004) and Gard (2006), respectively. Depth and velocity suitability criteria for juvenile Chinook were obtained from California Department of Fish and Game Stream Evaluation Report Number 05-1 (2005). Velocity, depth, and cover habitat suitability criteria were based on studies in California rivers, and substrate HSC were derived in Washington.

## 2.3 Results

Snorkel surveys of over 100,000 m<sup>2</sup> of habitat were performed on both the American River and Mokelumne River (Table 1) within and outside of the enhancement sites. In the American River, during these surveys, researchers observed 814 juvenile Chinook salmon and 157 juvenile steelhead. In the Mokelumne River 87 juvenile Chinook salmon and 301 juvenile steelhead were observed. These observations equate to 0.00447 Chinook m<sup>-2</sup> and 0.000862 steelhead m<sup>-2</sup> in the American River and 0.000858 Chinook m<sup>-2</sup> and 0.002969 steelhead m<sup>-2</sup> in the Mokelumne River. These fish densities are extremely low. These systems had poor spawner returns in previous years which likely led to depressed recruitment. These low densities also created challenges in obtaining sufficient numbers to characterize relationships between fish and their habitat. For each observation, researchers recorded characteristics of the habitat associated with the fish—these data were then used to parameterize models.

**Table 1: Summary of Total Area Surveyed**

<b>Snorkel Survey Results</b>		
	<b>American River</b>	<b>Mokelumne River</b>
Area surveyed (m <sup>2</sup> )	182,098	101,374
Average Water Temperature (°C)	16.4	14.7
Observations Chinook (<50 mm)	42	1
Observations Chinook (>50 mm)	62	26
Mean Chinook size (mm)	71	76
Observations steelhead (<50mm)	15	37
Observations steelhead (>50mm)	21	96
Mean steelhead size (mm)	64	75

Note: Average water temperature, average size and total number of juvenile Chinook and steelhead observations are listed below for each study river. We note that a single observation often consisted of a group of fish, all fish were <100mm.

Our hydraulic simulations covered a range of flows frequently observed in both the American and Mokelumne rivers. To develop a stage discharge relationship for each river we physically measured water surface elevations at 4 different discharges on the American River (1760, 1956,

3942, and 4653 CFS) and water surface elevations at 3 different discharges on the Mokelumne River (402, 1406, 1708 CFS). Using linear regression in program R (R Development Core Team, 2007) we estimated the stage discharge relationship for intermediate and greater discharges. This relationship is used, in part, to calibrate the hydraulic simulations in River 2D. Specifically the measured discharge is a key upstream parameter input and water surface elevation is a key input at the downstream end of the modeled reach. The methods described in Steffler and Blackburn (2002) state that a reasonable discrepancy between in the inflow and outflow shouldn't exceed 1 percent. A difference within 1 percent between the measured inflow and simulated outflow is indicative of a reasonable hydraulic solution, in combination with other model output (i.e. final solution change <math>< 10^{-4}</math>, Froude projections <math>< 1.0</math>, and limited hydraulic anomalies). The mesh quality index (QI) can influence the hydraulic solution so we attempted to keep this measure as consistent between models as possible and greater than 0.3. Tables 2 and 3 summarize some of the hydraulic model output for both rivers.

**Table 2: .Summary of the American River, River 2D, Hydraulic Model Solution Output**

American River: River 2D Simulated Output					
Discharge (CFS)	$\Delta$ final solution	QI	Inflow (m3/s)	Outflow (m3/s)	% Difference
1200	0.0675	0.383	33.98	34.02	0.12%
1760	0.000944	0.378	49.838	50.025	0.38%
1956	0.0388	0.383	55.388	55.603	0.39%
2500	0.00071	0.411	70.792	70.597	-0.28%
3100	0.00445	0.392	87.782	87.832	0.06%
3942	0.0119	0.383	111.625	111.664	0.03%
4653	0.00845	0.408	131.744	131.781	0.03%
5100	0.000008	0.418	144.416	144.446	0.02%
6000	0.00394	0.387	169.901	169.919	0.01%

Note: includes the modeled discharge, the final solution change, the mesh quality index (QI), the Inflow (m3/s), simulated Outflow (m3/s) and the percent difference between the Inflow (model input) and Outflow (simulated).

**Table 3: Summary of the Mokelumne River, River 2D, Hydraulic Model Solution Output**

<b>Mokelumne River: River 2D Simulated Output</b>					
<b>Discharge (CFS)</b>	<b>Δ final solution</b>	<b>QI</b>	<b>Inflow (m<sup>3</sup>/s)</b>	<b>Outflow (m<sup>3</sup>/s)</b>	<b>% Difference</b>
200	0.0000638	0.5038	5.664	5.67	0.11%
300	0.0119	0.4804	8.496	8.502	0.07%
402	0.0000331	0.393	11.385	11.386	0.01%
500	0.00012	0.518	14.16	14.161	0.01%
600	0.001977	0.436	16.992	16.992	0.00%
800	0.03606	0.5042	22.6559	22.657	0.00%
900	0.00167	0.482	25.488	25.489	0.00%
1000	0.01001	0.521	28.32	28.31	-0.04%
1100	0.000621	0.5027	31.152	31.154	0.01%

Note: includes the modeled discharge, the final solution change, the mesh quality index (QI), the Inflow (m<sup>3</sup>/s), simulated Outflow (m<sup>3</sup>/s) and the percent difference between the Inflow (model input) and Outflow (simulated).

## 2.4 Conclusions

The measured inflow and predicted outflow were reasonably close to each other (all differences between inflow and outflow were < 1 percent; Table 2 and 3) and as such it was determined that these models reasonably reflect the hydraulic conditions under the modeled discharges. There was a measureable amount of variation in the end solution change between models, indicating that some of the hydraulic models had not reached a stable solution according the standards proposed by Steffler and Blackburn (2002). This is likely due to one or more nodes in the computational mesh alternating between wet and dry status through different iterations of the hydraulic solution (Steffler and Blackburn 2002). The mesh and node density was high in both the American and Mokelumne systems and this may have increased the likelihood for this error to occur. It is important to note that the Froude measures in all model simulations were below 2.0 and below 1.0 across the majority of modeled space. In addition, researchers could not identify any anomalous velocity predictions across the modeled space. For these reasons, it is believed that the hydraulic models performed well and thusly were used in analysis and comparison of competing models.

# CHAPTER 3: Increasing Habitat Model Complexity

## 3.1 Methods

### 3.1.1 Escape Cover

In collaboration with the United States Fish and Wildlife Service, researchers collected topographic data in the enhanced side channel and adjacent habitats using a Topcon brand survey-grade RTK GPS. The task objectives were to enrich the existing topographic data set, identify zones of incision and deposition (as a result of the enhancement effort), and identify and delineate escape cover and dominant substrate across the modeled reach. Researchers combined the existing topographic data with the post enhancement topographic data after identifying, and excluding, zones of deposition and incision. These data were used as key parameter inputs in development of the River 2D model.

Dominant cover was assessed visually across the whole modeled reach. Polygons were created in ArcMap to delineate dominant substrate and cover types across the modeled reach. Each polygon included substrate and cover attributes encompassed within that polygon. Regions with homogenous substrate and cover were delineated by manually creating polygons (Editor, ArcMap) with a series of topographic points that bordered two substrate or cover types. Regions of highly heterogeneous substrate or cover were delineated by creating Thiessen polygons (Analysis, ArcMap). Both polygon types were merged in ArcMap and using the Spatial Join tool (Analysis, ArcMap) we assigned the attributes of each polygon to all the topographic points encompassed by that polygon for topographic data.

### 3.1.2 Bioenergetics

Following the methods described in Bratten et al (1997), Hayes et al. (2007), Hill and Grossman (1993), a bioenergetics-based suitability curve for water velocity was developed for the target species. To determine the relative energy available to drift-feeding salmonids, the abundance and mean weight of drifting invertebrates was estimated for the spring and summer in our study sites (see Titus et al. (in Prep) for detailed methods). The average energy content for each invertebrate order was derived from Cummins and Wuycheck (1971) and Luecke and Brandt (1993). An estimate of fish size and water temperature was calculated for the time period that the snorkel surveys were conducted and used as key parameter inputs (American River 4.65g and 16.4°C, Mokelumne 5.48g and 14.7°C). A bioenergetics model incorporating average fish size, water temperature, energy available from drifting invertebrates, energy costs associated with swimming and excretion was then developed. Specifically, a modified 'Wisconsin' bioenergetics model was used. This model can predict growth based on the temperature, consumption rates, and fish size. The energetic expenditure component of the bioenergetics model is influenced in an exponential fashion by the water velocity utilized by the individual fish, with higher velocities requiring higher energy expenditure. Furthermore, prey capture probability is influenced by water velocity, with capture probability decreasing at higher water velocities. However, higher water velocities also deliver food at a higher rate. All of these relationships were parameterized by the literature or from site-specific studies (see references above). Habitat suitability was defined as a proportion of the maximum growth potential given the aforementioned parameter estimates, where 100 percent of the growth potential at a given velocity had a suitability of 1.0.

### 3.1.3 Comparing Competing Models

Available habitat is based on the WUA (Bovee, 1982) which is calculated as the product of the composite suitability index (Steffler and Blackburn, 2002). Estimates of WUA were derived for Chinook salmon and steelhead trout in juvenile life stages for 9 flow regimes. WUA projections were plotted against flow and qualitatively compared the habitat-flow relationship.

## 3.2 Results

The WUA estimates across hydrodynamic habitat models varied substantially. In general, there was relationship between WUA and discharge. However, in some instances there was a negative relationship between increasing discharge of flow and WUA estimates while in other models there was a positive relationship. The habitat-flow relationship was linear in most cases, but some habitat suitability criteria produced a non-linear relationship between discharge and WUA projections. A summary of the WUA output and discharge modeled is provided below in Table 4 and Table 5.

**Table 4: .Summary of American River Hydrodynamic Habitat Model Output Including Discharge, Species, Model Type and WUA Estimate**

Discharge (CFS)	Species	LSHSC	SSHSC	LCHSC	SCHSC	BEHSC
1200	SH	8231.857	4544.868	5360.692	25807.834	1998.949
1760	SH	7431.939	4179.995	4867.215	24759.010	1559.822
1956	SH	7035.382	4058.916	4636.870	24414.275	1443.998
2500	SH	6143.437	3770.586	4167.255	23649.814	1334.165
3100	SH	5349.837	3505.768	3873.878	23138.627	1230.706
3942	SH	4301.488	3218.973	3736.711	22893.821	859.974
4653	SH	3688.715	3075.952	4126.542	23099.488	763.493
5100	SH	3317.515	3008.700	4332.445	23190.870	696.355
6000	SH	2829.289	2906.752	5044.304	23270.693	576.566
Discharge (CFS)	Species	LSHSC	SSHSC	LCHSC	SCHSC	BEHSC
1200	CH	11572.754	3464.131	4374.540	9310.010	3936.754
1760	CH	9142.549	2975.062	3852.117	8382.742	3032.125
1956	CH	8703.733	2853.455	3666.434	8165.884	2856.486
2500	CH	7505.615	2575.297	3514.303	7731.719	2572.758
3100	CH	6354.970	2359.966	3372.064	7599.643	2472.635
3942	CH	4986.807	2115.665	3220.611	7866.674	1660.659
4653	CH	4415.598	1972.713	3791.404	8546.829	1309.758
5100	CH	4389.768	1952.143	4063.798	9040.175	1208.429
6000	CH	4406.853	1993.867	4857.848	10140.178	1039.710

Note: Model type is abbreviate as follows, literature based HSC with substrate suitability (LSHSC), site specific HSC with substrate suitability (SSHSC), literature based HSC and cover suitability (LCHSC), site specific HSC with cover suitability (SCHSC), bioenergetics-based HSC (BEHSC).

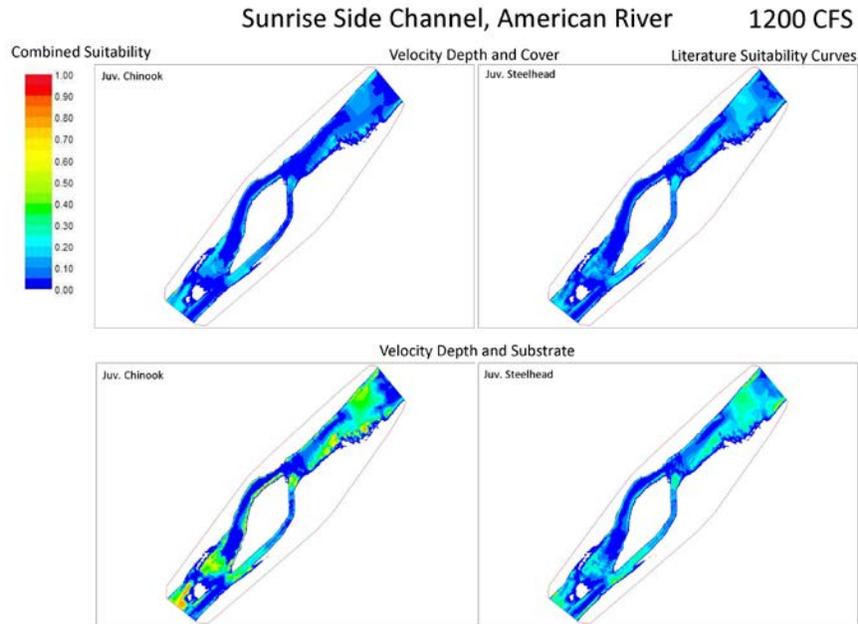
**Table 5: Summary of Mokelumne River Hydrodynamic Habitat Model Output Including Discharge, Species, Model Type and WUA**

Estimate Discharge (CFS)	Species	LSHSC	SSHSC	LCHSC	SCHSC	BEHSC
200	SH	771.654	2499.629	551.442	758.839	427.115
300	SH	868.582	2726.15	631.999	869.329	423.705
402	SH	924.116	2797.536	693.756	923.786	417.908
500	SH	957.282	2763.786	751.152	952.506	372.923
600	SH	980.678	2652.532	817.035	973.391	368.922
800	SH	957.234	2323.53	874.694	972.488	321.154
900	SH	923.426	2153.913	880.305	962.988	310.505
1000	SH	888.794	2007.37	885.312	962.094	304.864
1100	SH	851.284	1892.85	885.201	968.004	286.066
Discharge (CFS)	Species	LSHSC	SSHSC	LCHSC	SCHSC	BEHSC
200	CH	2107.489	282.969	914.031	1352.348	1150.826
300	CH	2150.309	289.559	938.076	1407.261	1113.173
402	CH	2113.591	285.712	950.736	1440.737	1056.596
500	CH	2018.24	275.283	951.173	1452.149	893.935
600	CH	1937.73	263.304	962.802	1463.709	840.443
800	CH	1705.135	232.206	929.726	1447.891	681.831
900	CH	1600.632	217.323	897.425	1436.152	653.854
1000	CH	1504.574	204.552	869.999	1435.833	645.755
1100	CH	1437.844	194.951	850.027	1439.34	623.735

Note: Model type is abbreviate as follows, literature based HSC with substrate suitability (LSHSC), site specific HSC with substrate suitability (SSHSC), literature based HSC and cover suitability (LCHSC), site specific HSC with cover suitability (SCHSC), bioenergetics-based HSC (BEHSC).

Modeling habitat suitability of different models on the two salmonid species in the two rivers provided visual maps of suitable habitat. For example, for the American River at the low flow level (1200 cfs), the most suitable habitat included area above the side channel on river left as well as toward the tail of the side channel. The margins of the side channel provided only a small edge of suitable habitat , Figure 1.

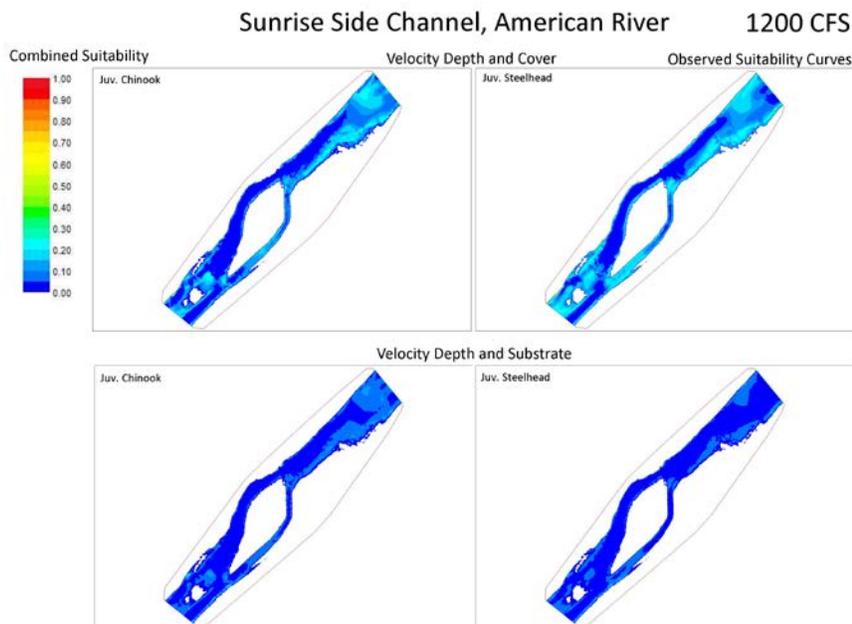
**Figure 1: American River (1200CFS) Combined Suitability Comparisons with Data Derived from Various Literature Sources**



Note: A comparison of combined suitability for juvenile Chinook (left panels) and juvenile steelhead (right panels) between models using either substrate or escape cover in conjunction with depth and velocity suitability criteria. These habitat criteria are derived from various literature sources. Note the direction of flow is from the top right of each panel to the bottom left for this and the following figures.

Using the suitability curves that were site-specific provided roughly similar results (Figure. 2). The two sets of parameters identified roughly similar habitats as being most appropriate for the two species. River left upstream of the island continued to be identified by the model as a good habitat for both juvenile Chinook salmon and steelhead.

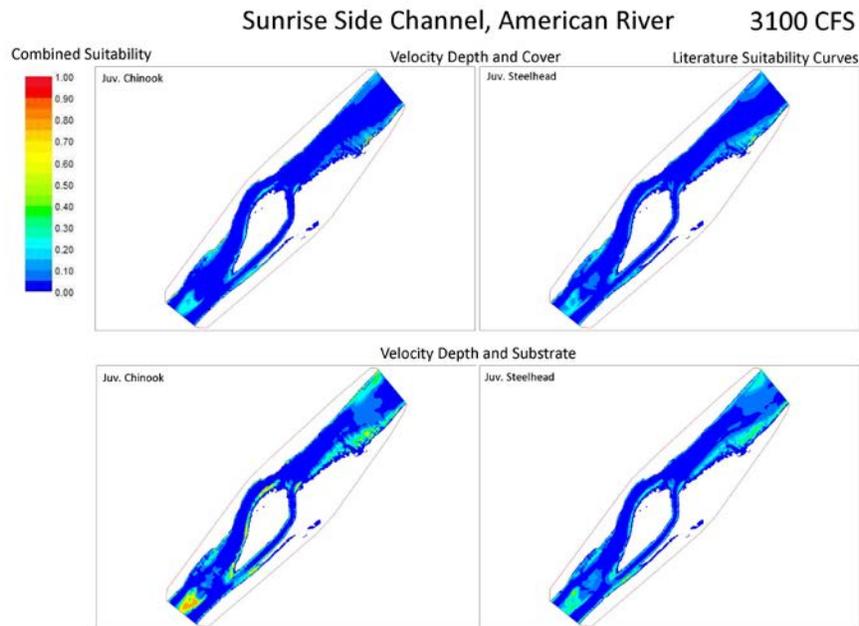
**Figure 2: American River (1200CFS), Combined Suitability Comparisons with Data Derived from Site Specific Habitat Use**



Note: Comparison of combined suitability for juvenile Chinook (left panels) and juvenile steelhead (right panels) between models using either substrate or escape cover in conjunction with depth and velocity suitability criteria. These habitat criteria are derived from site specific habitat use data.

Running these models on contrasting flow regimes illustrates that changing flows also changed the habitat that was predicted to be best for these juvenile salmonids. For example, on the American River at higher flows (3100 cfs), the habitat at the top of the island ceased to be identified as ideal habitat. At higher flows, the model predicted that this habitat would no longer be as suitable for salmonids, probably because higher flows increased the water velocity past the points that are most suitable for fish at this location. Instead, the bottom on the island was predicted to be suitable habitat as well as the submerged gravel bar that extends from the river left shore towards the downstream side of the island (Figure 3).

**Figure 3: American River (3100CFS), ) Combined Suitability Comparisons with Data Derived from Various Literature Sources**

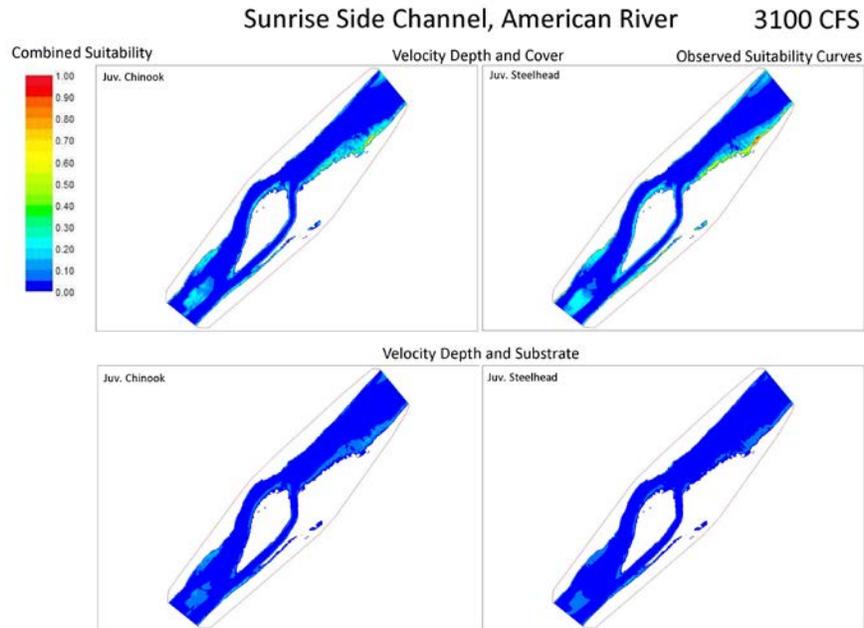


Note: Comparison of combined suitability for juvenile Chinook (left panels) and juvenile steelhead (right panels) between models using either substrate or escape cover in conjunction with depth and velocity suitability criteria. These habitat criteria are derived from various literature sources.

Similar to the results for the low flow habitat modeling, using literature vs. observed suitability curves led to different predictions. The different models identified roughly similar habitats as being the most suitable, but the amount of suitable habitat varied from model to model (compare Figures 3 and 4).

Analyzing the different types of habitat that are suitable at different flows highlights the dynamic nature of “what is good habitat for salmonids”. As flow regimes change, different aspects of the habitat change. Most notable, velocities will change and modify the location of suitable habitat. As the river rises and inundates more of the flood plain, more habitats will become available. For example, in comparing flows at 1200, 3100, and 6000 cfs (Figures. 1, 3, and 5), the suitable habitat changes completely. These modeling exercises allow predictive visualization of how different river morphologies will interact with varying flow regimes to drive the location and amount of suitable habitat for juvenile salmonids.

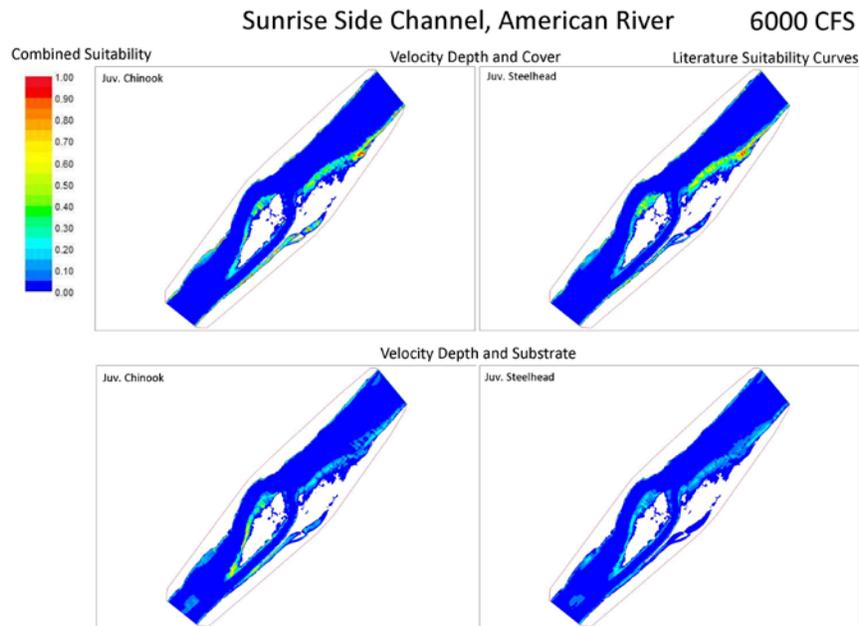
**Figure 4: American River (3100CFS), Combined Suitability Comparisons with Data Derived from Site Specific Habitat Use**



Note: Comparison of combined suitability for juvenile Chinook (left panels) and juvenile steelhead (right panels) between models using either substrate or escape cover in conjunction with depth and velocity suitability criteria. These habitat criteria are derived from site specific habitat use data.

Across these different species and rivers, we consistently found that the parameters that were included in the model were very influential in driving the type and location of suitable habitat. For example, the predictions from literature-derived curves versus observed suitability curves (Fig. 5 vs. Fig. 6) resulted in some differences but they are not large in magnitude. In contrast, whether the model includes cover or substrate will drive large differences in the location and amount of suitable habitat. On one hand, this result is somewhat reassuring as it indicates some level of consistency between literature and observation-based habitat suitability. Alternatively, this result also highlights that the models can be sensitive to the choice of input parameters.

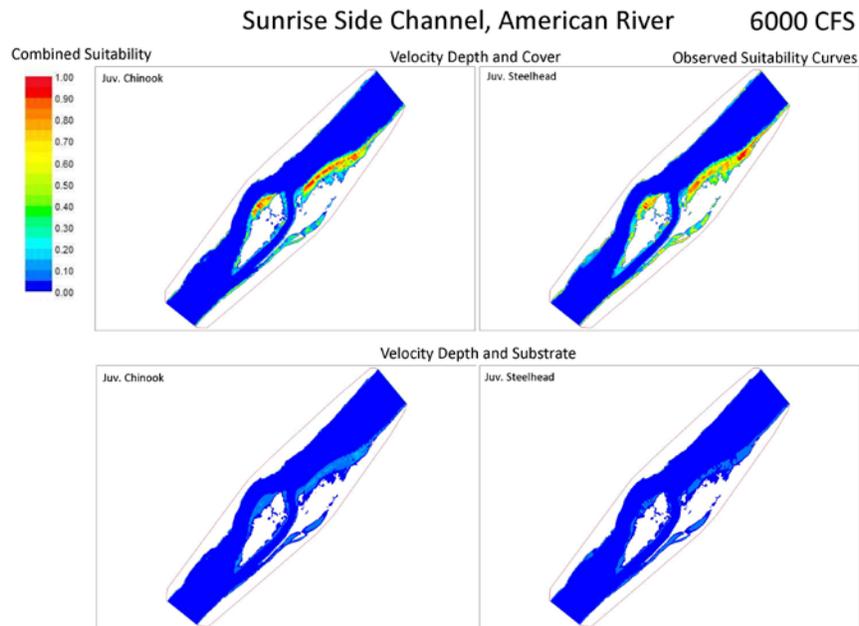
**Figure 5: American River (6000CFS), ) Combined Suitability Comparisons with Data Derived from Various Literature Sources**



Note: Comparison of combined suitability for juvenile Chinook (left panels) and juvenile steelhead (right panels) between models using either substrate or escape cover in conjunction with depth and velocity suitability criteria. These habitat criteria are derived from various literature sources.

Based on these graphical predictions of where suitable habitat is, it also appears that the habitats for both juvenile Chinook and juvenile steelhead are qualitatively similar. Both species tended to prefer the habitats along the margins of the rivers, with preferred habitat characteristics being roughly similar across the two species. One implication of this result is the prediction that both species of salmonids respond roughly similarly to changes in habitat. In the American River, increasing habitat for one species will likely increase habitat for the other species; but the reciprocal is also likely true, decreasing habitat for one species will likely decrease habitat for the other species.

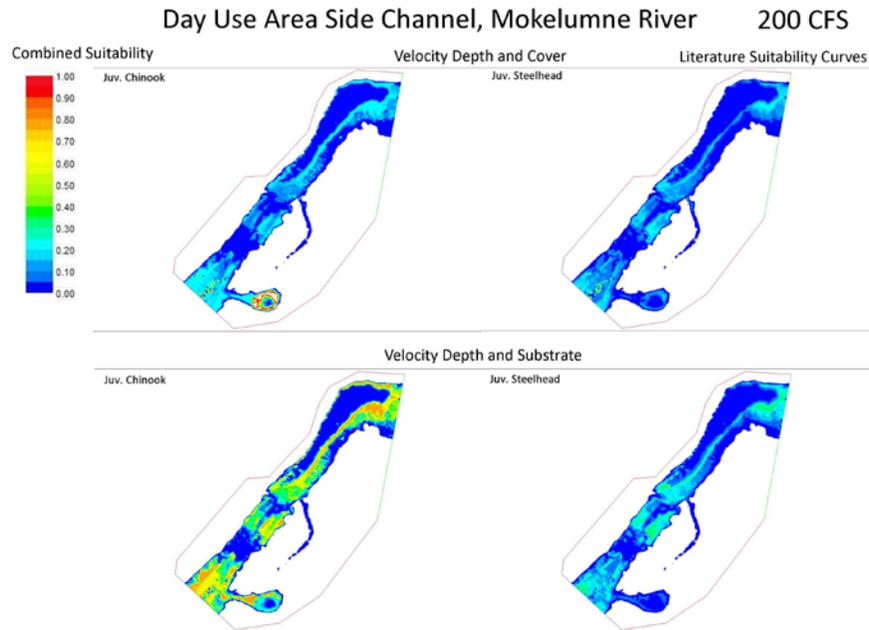
**Figure 6: American River (6000CFS), Combined Suitability comparisons with Data Derived from Site Specific Habitat Use**



Note: a comparison of combined suitability for juvenile Chinook (left panels) and juvenile steelhead (right panels) between models using either substrate or escape cover in conjunction with depth and velocity suitability criteria. These habitat criteria are derived from site specific habitat use data

Model projections from the Mokelumne River demonstrate similar patterns with both flow regime and model type driving different suitable habitat predictions. For the low flow prediction (200 cfs), the models identified several habitats with high suitability. For example, at the outflow of the side channel there is predicted to be an area with relatively high suitability. In addition, areas just to the river left of the upstream of the day use area are predicted to be suitable (Fig. 7). As was observed on the American River models, there are large differences in the amount and, to a lesser extent, the location of habitat, depending on the parameters that are used. Specifically, whether escape cover or sediment was included often drove fairly large differences. These differences are especially apparent in the Mokelumne River likely because there was quite a bit of woody debris and other cover within this reach.

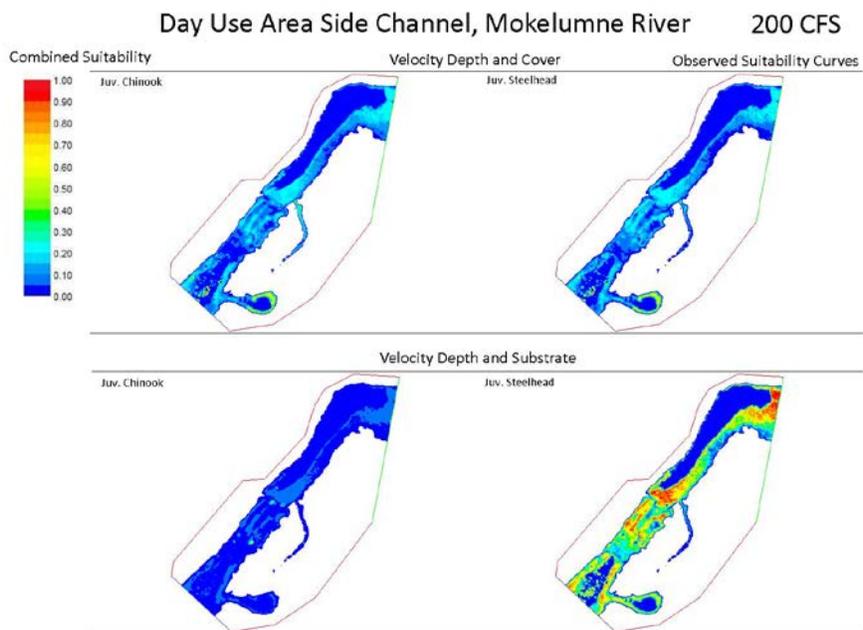
**Figure 7: Mokelumne River (200CFS), ) Combined Suitability Comparisons with Data Derived from Various Literature Sources**



Note: Comparison of combined suitability for juvenile Chinook (left panels) and juvenile steelhead (right panels) between models using either substrate or escape cover in conjunction with depth and velocity suitability criteria. These habitat criteria are derived from various literature sources.

One large difference between suitability curves generated from literature versus those generated from project observations is the amount of predicted habitat for Chinook salmon. Specifically, the suitability for WUA estimate for juvenile Chinook that was generated based on researcher's observations was lower than the WUA estimates from the literature based HSC (Figure. 7 and Figure. 8). This pattern is likely in part because researchers with this project didn't observe many Chinook salmon juveniles on the Mokelumne River during their snorkeling surveys, thus virtually all habitat is being characterized as not being suitable for Chinook.

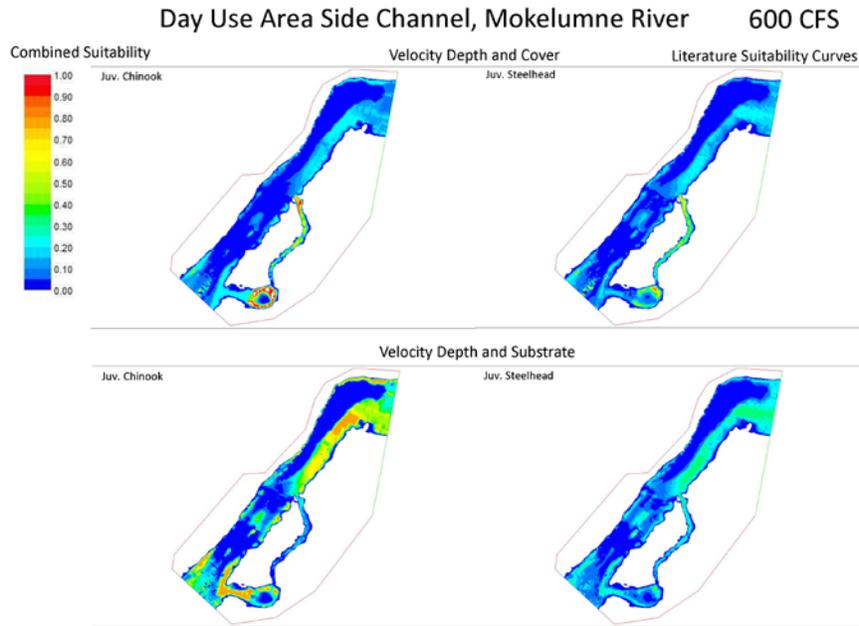
**Figure 8: Mokelumne (200CFS), Combined Suitability Comparisons with Data Derived from Site Specific Habitat Use**



Note: Comparison of combined suitability for juvenile Chinook (left panels) and juvenile steelhead (right panels) between models using either substrate or escape cover in conjunction with depth and velocity suitability criteria. These habitat criteria are derived from site-specific habitat use data.

One important change in salmonid habitat that occurs in the Mokelumne River as the discharge increases is the inundation of the side channel. According to this project's hydrologic model, this inundation appears to occur between 200 and 600 cfs (Figures 7, 8, 9, and 10). Although it varies with the different model formulations, this side channel is characterized to have suitable habitat for juvenile salmonids. Model formulations that include cover rank this side channel as especially high quality habitat (Figures 8 and 9). Not surprisingly, when the side channel does not have water flowing through it, it is not identified as good habitat for juvenile salmonids. Thus, a likely important threshold in discharge for the Mokelumne River is identified as occurring where the amount and location of suitable habitat changes substantially.

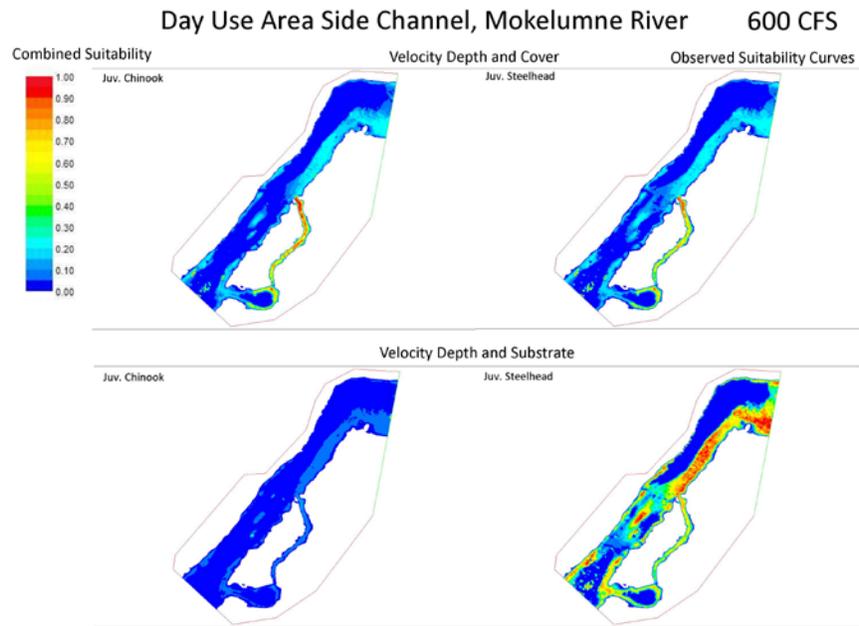
**Figure 9: Mokelumne (600CFS), ) Combined Suitability Comparisons with Data Derived from Various Literature Sources**



Note: Comparison of combined suitability for juvenile Chinook (left panels) and juvenile steelhead (right panels) between models using either substrate or escape cover in conjunction with depth and velocity suitability criteria. These habitat criteria are derived from various literature sources.

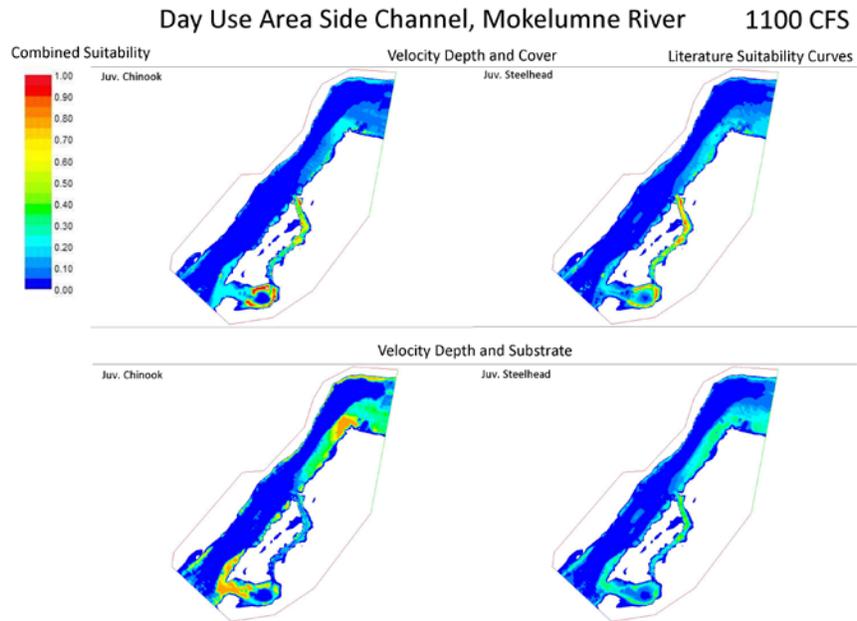
The location of suitable habitat changes substantially across the different discharges in the Mokelumne River. The side channel inundation opens up new habitat at higher discharges (~600 cfs). Concordantly, as flows increase, the main channel of the Mokelumne becomes less suitable for juvenile salmonids. At low flows, substantial areas were identified in the main channel as being good, larger gravel bars and other features generated preferred combinations of velocity and depth (Figures 7 and 8). However, as flows increased, especially at 1100 cfs, this habitat in the main channel ceased to be identified as high quality habitat. Although there is some habitat along the margins, the bulk of the habitat that is identified as suitable is located in the side channel. This side channel may provide critical fish habitat at higher flows. Figures 7 through 12 of the different appropriate habitat at different flow regimes facilitate visualization of the dynamic nature of suitable habitat for juvenile salmonids.

**Figure 10: Mokelumne (600CFS), Combined Suitability Comparisons with Data Derived from Site Specific Habitat Use**



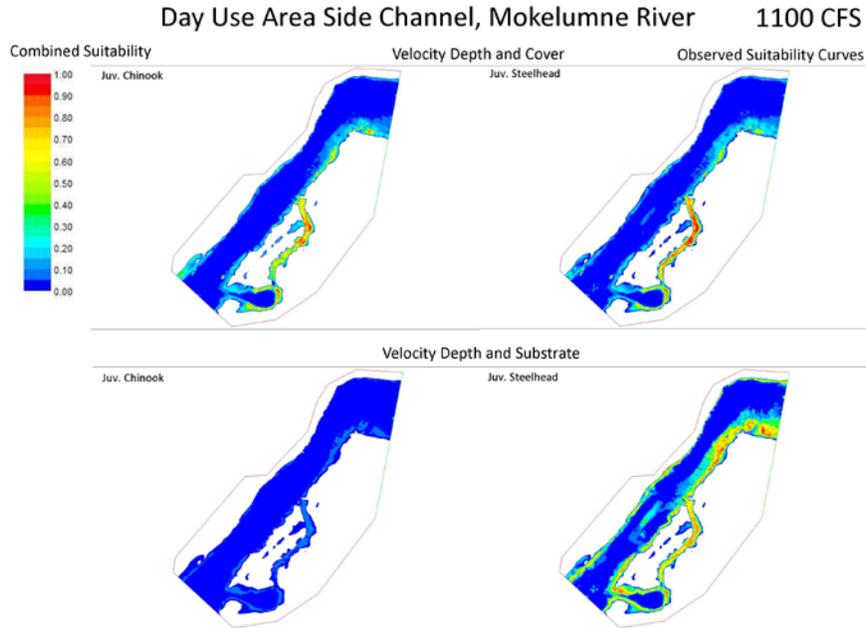
Note: Comparison of combined suitability for juvenile Chinook (left panels) and juvenile steelhead (right panels) between models using either substrate or escape cover in conjunction with depth and velocity suitability criteria. These habitat criteria are derived from site specific habitat use data.

**Figure 11: Mokelumne (1100CFS), ) Combined Suitability Comparisons with Data Derived from Various Literature Sources**



Note: Comparison of combined suitability for juvenile Chinook (left panels) and juvenile steelhead (right panels) between models using either substrate or escape cover in conjunction with depth and velocity suitability criteria. These habitat criteria are derived from various literature sources..

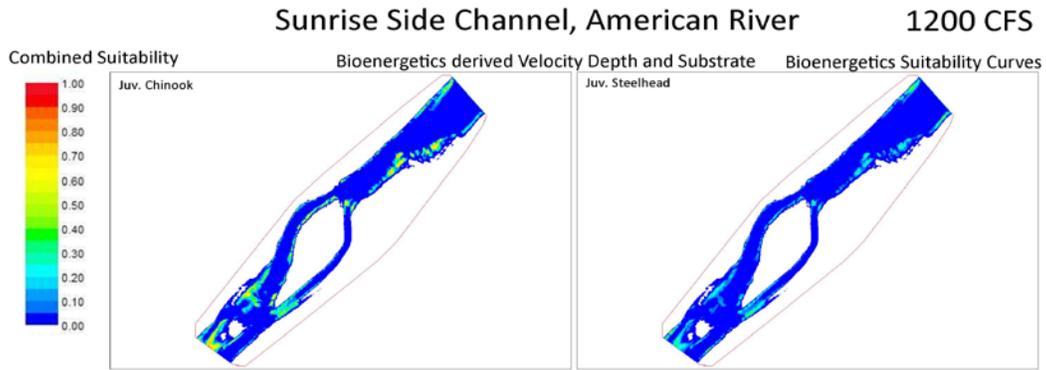
**Figure 12: Mokelumne (1100CFS), Combined Suitability Comparisons with Data Derived from Site Specific Habitat Use**



Note: Comparison of combined suitability for juvenile Chinook (left panels) and juvenile steelhead (right panels) between models using either substrate or escape cover in conjunction with depth and velocity suitability criteria. These habitat criteria are derived from site specific habitat use data.

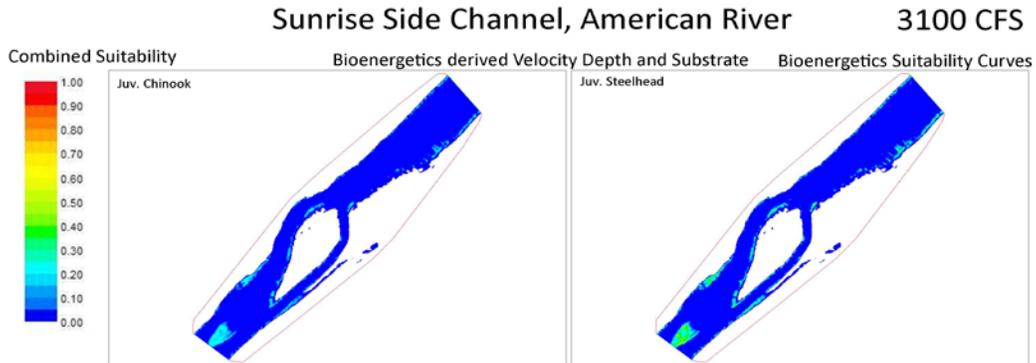
A bioenergetics habitat suitability curve was developed that incorporates both temperature and prey abundance as inputs. Through using site-specific information on prey density and published information on their caloric content, researchers were able to use this HSC to predict appropriate habitat. In general, the qualitative predictions of the bioenergetics-based hydrodynamic habitat models of the location of suitable habitat (Figures 13 through 18) were fairly similar to those of the other model constructions (Figures 1 through 12). For the American River, the model identified preferred habitat to be at river left upstream of the island and on the submerged gravel bar on river left on the downstream edge of the island. Increasing the discharge similarly changed the location of preferred habitat, reducing the patch of preferred habitat at the head of the island (Figures 13, 14, and 15).

**Figure 13: American (1200CFS), ) Combined Suitability Comparisons with Data Derived from a Bioenergetic-Based Model**



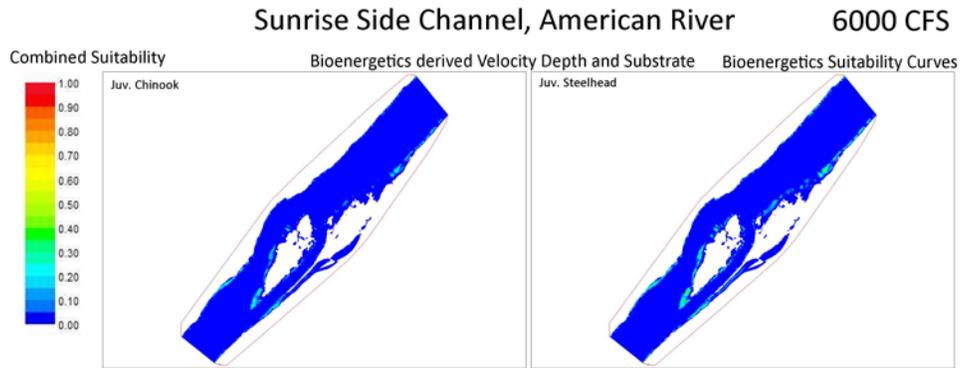
Note: Comparison of combined suitability for juvenile Chinook (left panel) and juvenile steelhead (right panel). These habitat criteria are derived from a bioenergetic-based model.

**Figure 14: American (3100CFS), ) Combined Suitability Comparisons with Data Derived from a Bioenergetic-Based Model**



Note: Comparison of combined suitability for juvenile Chinook (left panel) and juvenile steelhead (right panel). These habitat criteria are derived from a bioenergetic-based model.

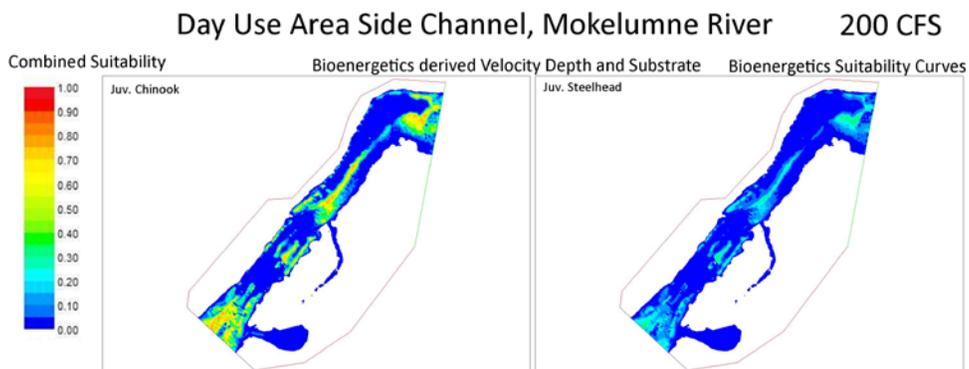
**Figure 15: American (6000CFS), ) Combined Suitability Comparisons with Data Derived from a Bioenergetic-Based Model**



Note: Comparison of combined suitability for juvenile Chinook (left panel) and juvenile steelhead (right panel). These habitat criteria are derived from a bioenergetic-based model.

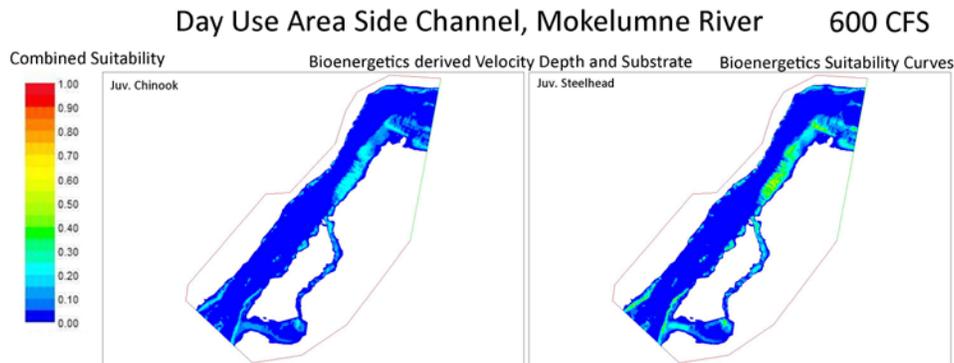
Incorporating bioenergetics into the model also allowed the visualization of preferred habitat for the Mokelumne River. As flows increased the location of the preferred habitat shifted from the main channel area at the head of the side channel to the habitat that was actually within the side channel (Figures 16 through-18). However, the predictions from the bioenergetics gave different estimates of total weighted usable area at different discharges.

**Figure 16: Mokelumne (200CFS), ) Combined Suitability Comparisons with Data Derived from a Bioenergetic-Based**



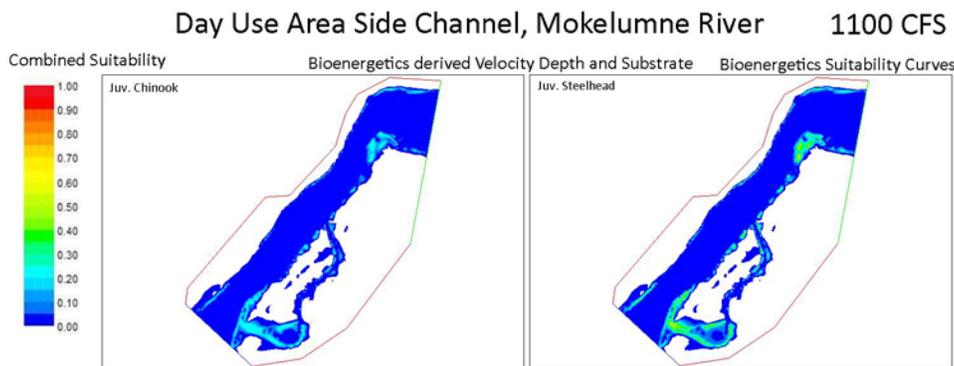
Note: Comparison of combined suitability for juvenile Chinook (left panel) and juvenile steelhead (right panel). These habitat criteria are derived from a bioenergetic-based model.

**Figure 17: Mokelumne (600CFS), ) Combined Suitability Comparisons with Data Derived from a Bioenergetic-Based Model**



Note: Comparison of combined suitability for juvenile Chinook (left panel) and juvenile steelhead (right panel). These habitat criteria are derived from a bioenergetic-based model.

**Figure 18: Mokelumne (1100CFS), ) Combined Suitability Comparisons with Data Derived from a Bioenergetic-Based Model**

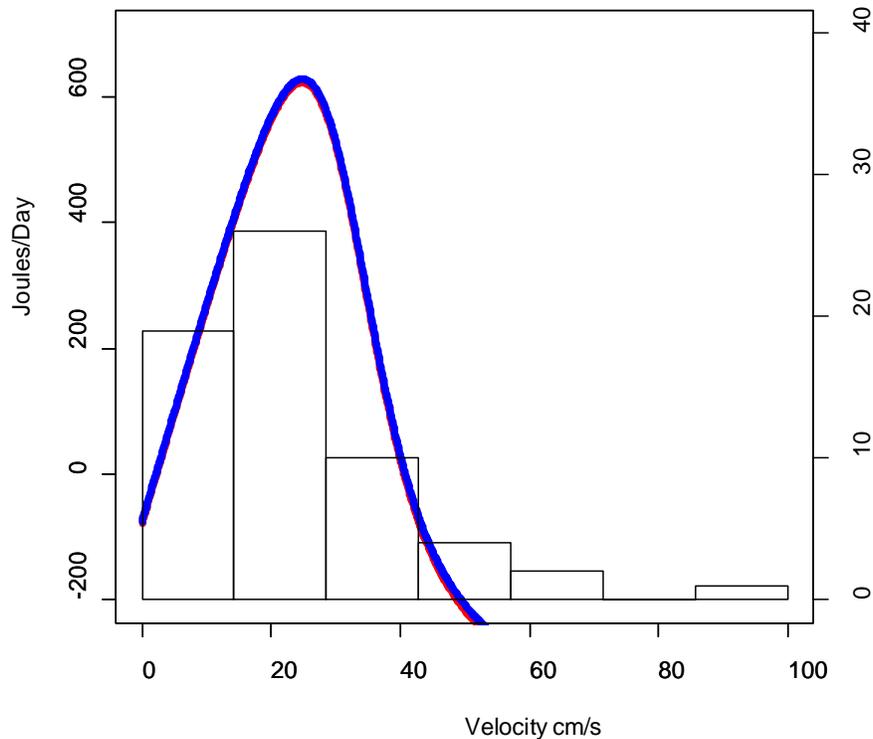


Note: comparison of combined suitability for juvenile Chinook (left panel) and juvenile steelhead (right panel). These habitat criteria are derived from a bioenergetic-based model.

One of the strengths of using a bioenergetics approach to create a habitat suitability curve is that it more directly incorporates the potential costs and benefits of a given habitat choice. A bioenergetics-derived curve will shift the preferred velocity depending on the food density and the temperature (Figure 19). This approach does not assume a constant preferred velocity, regardless of the stream temperature and density of potential food items in the stream drift. Bioenergetics modeling predicts that juvenile salmonid growth will peak at intermediate velocities of approximately  $25 \text{ cm s}^{-1}$ . At this velocity, food delivery will provide ample resources for growth but the energetic cost of maintaining position in the water column will not

be too exorbitant. Researchers made the realistic assumption that the velocity that maximizes their growth will be the preferred habitat. This type of bioenergetics approach may be more flexible to a variety of circumstances, where changes in temperature and food abundance change the most beneficial water velocity.

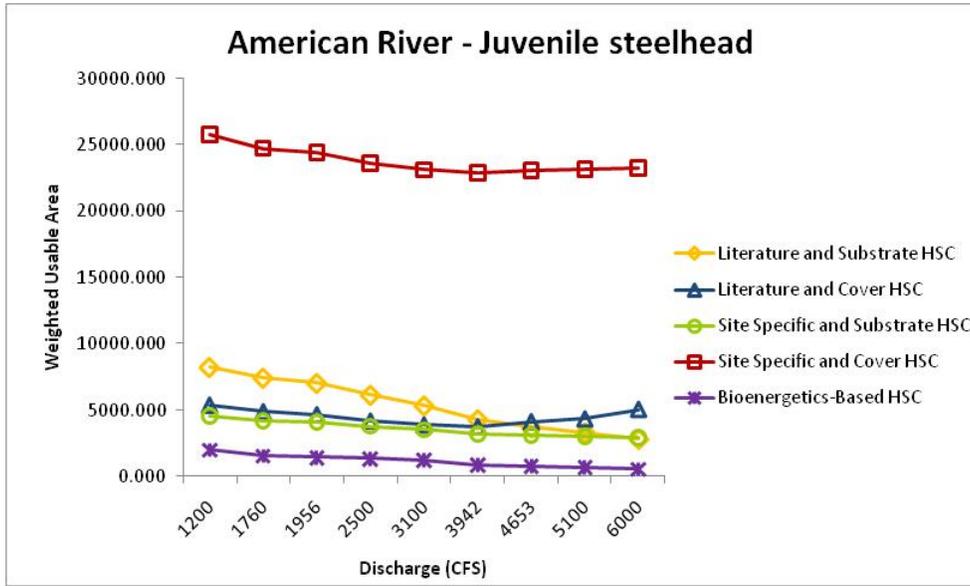
**Figure 19: Relationship Between Net Energy Gain as a Function of Food Availability and Velocity**



Note: For the American (red line) and Mokelumne (blue line) rivers. Plotted (right axis corresponds to fish observed at a given velocity bin) is a histogram of the frequency of observed velocity use by Chinook juveniles in the American River.

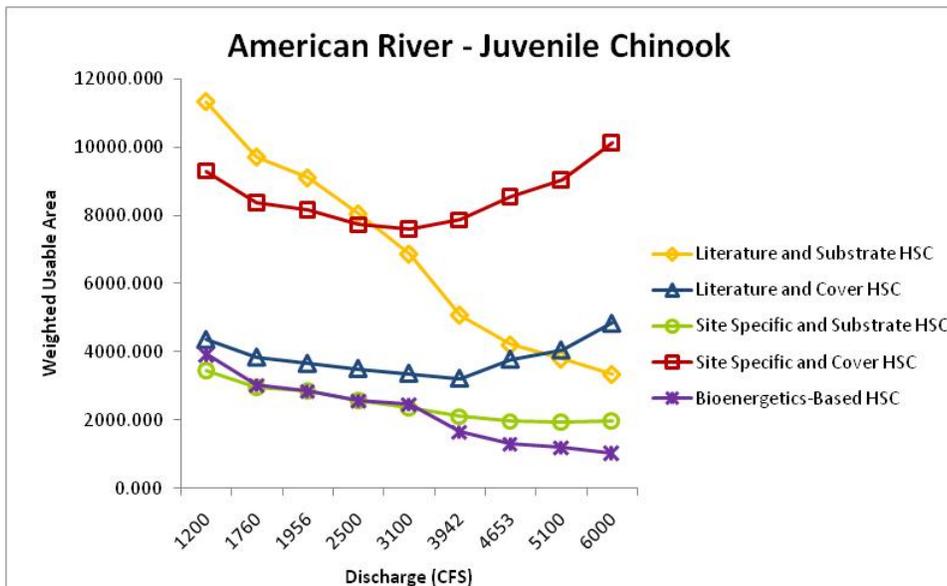
The food availability between these two rivers for the time period modeled is very similar, thus the model predictions are similar. It is important to note that there are considerable differences across seasons for the two rivers. Also plotted in Figure 19 is a histogram of observed habitat use (velocity) for Chinook in the American river. The bioenergetics-based model explained almost 80 percent of the observed habitat use.

**Figure 20: Comparison of Models for American River Juvenile Steelhead**



WUA was calculated for each model scenario across 9 flow regimes. This weighted usable area is a sum of habitat, weighted by its estimated suitability. This metric is a quantification of the amount of habitat available for juvenile salmonids. There were large differences in WUA across discharges and model formulations (Figures 20, 21, 22 and 23). For steelhead in the American River the most important factor was the model formulation. Different modeling formulations drove large differences in the estimation of WUA. Flow regime also altered WUA. Specifically, as discharge increased, WUA generally decreased slightly. While there is more water at higher discharges, there is not always more suitable habitat as fish habitat may become limited to the margins of the river (Figures 13 through 15).

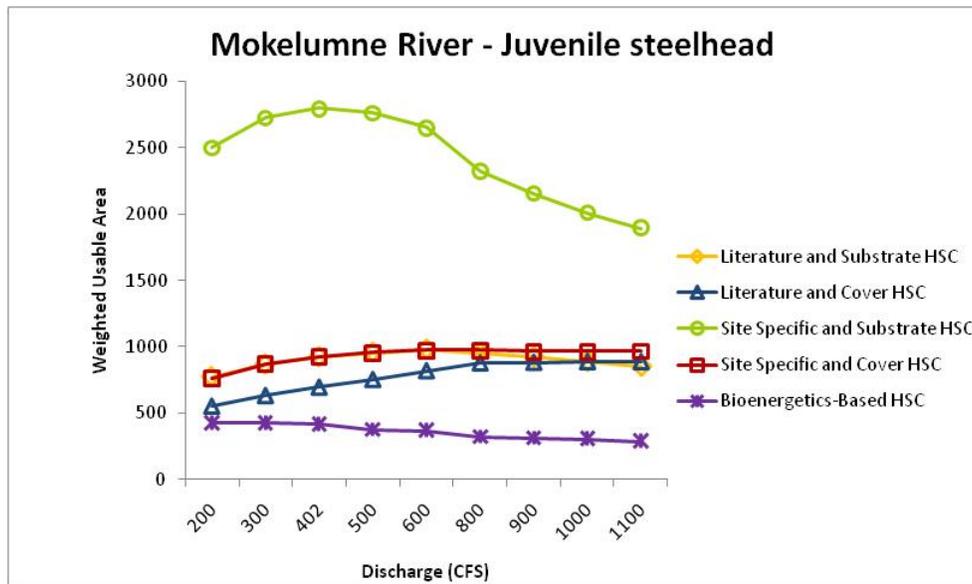
**Figure 21: Comparison of Models for American River Juvenile Chinook**



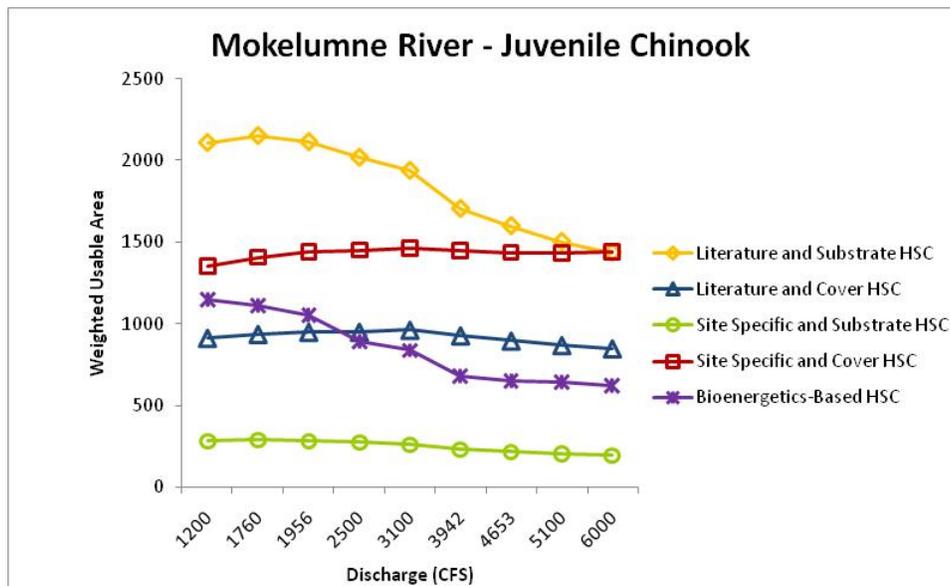
Projections of WUA for Chinook salmon juveniles in the American River were fundamentally different. Similar to steelhead, model type made a large difference in overall amount of WUA. However, the WUA changed more as a function of discharge. The type of model formulation dramatically altered these patterns. The model with substrate and literature HSC estimated that with increasing discharge there would be a threefold decrease in WUA. In contrast, both models with cover in them showed an increase in WUA at discharges above 3100 cfs. Models with cover likely exhibit this pattern because as the river discharges increases, more of the channel will be inundated and the margin habitats will start to contain cover in the form of riparian vegetation such as willows. These results also communicate the critical result that the choice of model could fundamentally alter even the qualitative predictions of relationships between discharge and habitat. Does increasing discharge increase or decrease salmonid habitat? The answer to this basic but critical question depends upon the model formulation.

Weighted usable area estimates for the Mokelumne River also demonstrated dramatic differences between model formulations (Figures 22 and 23). Similar to the American River, different models predicted vastly different amounts of weighted usable area. The amount of usable habitat also changed as a function of discharge. Again, this depended on model formulation. For juvenile steelhead, the model that included substrate and site specific HSC predicted that the most habitat would be found at discharges of ~ 400 cfs. Three of the other models all predicted that weighted usable area would increase as discharge increased. Some of this gain in weighted usable area is likely due to the inundation of the side channel. The Mokelumne River side channel may help keep substantial amounts of preferred types of habitat at higher discharges. Juvenile Chinook in the Mokelumne River tended to have slight decreases or no change in WUA associated with increased discharge (Figure 23).

**Figure 22: Comparison of Models for Mokelumne River Juvenile Steelhead**



**Figure 23: Comparison of Models for Mokelumne River Juvenile Chinook**



### 3.3 Conclusions

A series of models were formulated and applied to map and quantify suitable habitat for juvenile Chinook salmon and steelhead trout in the American and Mokelumne River. During the study, juvenile salmon were observed at exceedingly low densities (between 0.000858 and 0.00447 fish m<sup>-2</sup>), highlighting the status of salmonids in these rivers. Mapping out suitable habitat provided key visualization of the location of suitable habitat for juvenile salmon across different flow regimes. The location of suitable habitat was variable, but was often identified as margin habitat or on riverine features such as gravel bars or at the head or tails of islands. The location of preferred habitat varied substantially among different flows and life stages. These visualizations illustrate the dynamic nature of salmon habitat. Channel morphology will define how different flow regimes alter habitat. In these highly controlled systems, where dam operators control river flows and restoration engineers change the river morphology, collaboration between these groups will help facilitate the management of these systems. For example, in the Mokelumne River, the side channel was characterized as providing high quality salmon habitat at flows at or above 600 cfs. At lower discharge the side channel was not inundated.

Different habitat suitability data and inputs produced fundamentally different model projections and predictions. There were differences in whether literature-based or observation-based habitat suitability curves were used. The decision of whether to include, for example, cover or substrate, often made a substantial difference in the location and amount of suitable habitat. Perhaps most illuminating was that the difference between models that included cover or not exhibited fundamentally different relationships between discharge and weighted usable area on the American River. Models that included cover exhibited an increase in WUA above an intermediate discharge (3100 cfs). Indeed, highest discharges had approximately 20 percent more identified habitat than intermediate discharges. This pattern was fundamentally different for models that did not include cover but rather included substrate. For these models, WUA only decreased as discharge increased. One model predicted a decrease in WUA by over 60

percent as discharge increased. Clearly, even at the most coarse scale, the results depend critically on and are sensitive to the formulation of the model and the species in question.

# CHAPTER 4: Selecting the Best Habitat Model Using AIC

## 4.1 Methods

The effects of velocity, depth, adjacent velocity, substrate, escape cover, and mean water temperature on habitat use were analyzed for a subset of our direct observation data using a series of generalized linear models implemented in R (R Development Core Team 2007). AIC scores (Akaike 1974; Hurvich and Tsai 1989; Burnham and Anderson 2002) were used to compare different habitat use models as a binomial function of velocity, depth, adjacent velocity, substrate, escape cover, and mean water temperature. Researchers compared the most complicated model (all possible submodels) to determine which predictor variables best explained variation in habitat use.

AIC was used as a formal framework for model selection to determine which variables were most important in explaining habitat use. The AIC score of any particular model can identify the best model out of the suite--the model producing the lowest AIC score best explains variation in the dependent variable with the least number of independent variables. A difference of 2 AIC units between models can be interpreted as evidence for model superiority. To examine the relative importance of each parameter a subset of juvenile Chinook data (41 observations) collected on the American River was analyzed. These particular observations were used in this analysis because there were of similar sized fish and were the only observations that contained complete data for the parameters we aimed to compare. Table 6 identifies the mean and standard error of each parameter included in the analysis.

**Table 6: Mean and +/- S.E. of Data used in AIC Analysis for American River Chinook.**

Parameter	Mean	+/- S.E.
Temperature (°C)	16.441	0.090
Depth (m)	0.378	0.011
Velocity (m/s)	0.308	0.016
Adjacent Velocity (m/s)	0.376	0.019
Substrate Diameter (m)	0.068	0.002
Escape Cover (A/B)	NA	NA

Note escape cover was categorical and identified as A (substantial cover) or B (little, or no cover). Included are 41 occupied habitat units and 300 randomly identified unoccupied habitat units. All parameters in AIC analysis were measure at occupied and unoccupied locations

## 4.2 Results

Through comparing a suite of competing models, researchers quantitatively asked the question: what factors should be included in models? This examination is critical given our results that

model outputs are both quantitatively and qualitatively sensitive to the formulation of the model (see previous sections). We compared 36 competing models. The data identified a group of five possible models as being the most parsimonious with the data. The best model was one that included velocity, depth, temperature, and adjacent velocity. The top five models all included velocity, temperature, and adjacent velocity (Table 7). This consistency is strong evidence for the importance of these parameters in predicting fish habitat. This also revealed that the best single factor models were temperature, and then velocity, evidence of their importance as drivers of suitable fish habitat.

The factors of cover and substrate were not consistently identified in the top models (Table 7). Cover was supported in two of the top five models and substrate was a factor in two different top models. The data did not show strong support for the inclusion or exclusion of these factors. The inclusion of cover versus substrate was enormously important for defining the habitat of juvenile Chinook salmon in the American River (Figure 21). In all likelihood, the projections of high discharge entail extrapolations of relationships between cover and fish. Model selection does not reduce all of the uncertainty in relationships between discharge and habitat.

**Table 7: Results of the AIC Analysis: Each Model Compared with Degrees of Freedom (df) and AIC Score**

Model	df	AIC	Model	df	AIC
V + D + T + AV	9	215.18	T + S	5	242.69
V + D + T + AV + S	11	216.06	T + C	4	243.55
V + T + AV + S	9	216.29	V	3	244.06
V + T + AV + C	8	216.92	V + D	5	244.18
V + D + T + AV + S + C	12	217.93	V + C	4	245.67
V + D + AV	7	224.04	V + D + C	6	245.72
V + AV	5	225.87	V + S	5	246.10
V + T	5	234.73	V + D + S	7	246.12
V + D + T	7	235.99	D + AV	5	247.64
D + T + AV + S + C	10	239.60	D + AV + S + C	8	247.66
D + T + AV	7	239.87	D	3	250.06
D + T	5	240.45	AV + S	5	250.71
T + AV + S	7	240.77	AV	3	251.44
D + T + S	7	241.05	D + S	5	251.47
T + AV	5	241.59	D + C	4	251.88
D + T + C	6	241.94	AV + C	4	252.74
T	3	241.98	S	3	254.73
T + AV + C	6	242.55	S + C	4	256.73

Note: Model parameters are as follows, velocity (V), depth (D), adjacent velocity (AV), substrate (S), escape cover (C), and water temperature (T). Note that there are two sets of columns for the different models. Highlighted models are the top five models that are substantially more parsimonious with the data than the other competing models.

### 4.3 Conclusions

The model comparison indicates that the most parsimonious model of habitat use on the American River includes velocity, depth, adjacent velocity, and water temperature. It is important to note that the top five models, although very close in effectiveness, all include velocity, temperature, and adjacent velocity. This is evidence that these three factors are important parameters defining habitat selection by juvenile Chinook salmon. Of particular note is evidence for the importance of water temperature. Currently, many hydrodynamic habitat models do not include water temperature in the habitat model. Given that fish such as these juvenile Chinook salmon are ectothermic, water temperature will control their physiological rates and processes. As temperature increases, fish will have to consume more food to keep their growth constant. Furthermore, at warmer temperature, fish have increased rates of physiologic processes including growth. At the crudest scale, too high of temperatures can be lethal, and these threshold temperatures are not that high for salmonids. For example, off channel habitats that would otherwise be suitable habitats may have insufficient water flow to keep water cool and thereby prevent this habitat from being suitable for salmonids. Thus, temperature is likely critical in influencing how fish assess habitat. Other studies (for example, Hill and Grossman 1993) have illuminated the effectiveness of a bioenergetics approach to modeling habitat quality. It has been demonstrated in this study that water temperature is clearly important and can be included in the habitat model either by directly having temperature as a factor or by utilizing a bioenergetics-based habitat suitability criteria.

Many methods of calculating habitat suitability have been criticized for treating each parameter as equally important and independent. These AIC results support this criticism. None of the models using a singular parameter received much support. It is also important to note that of the models that only included a single predictor variable, the model including water temperature received the most support further supporting the importance of water temperature in habitat selection. These results also emphasize that there are many factors that can be important in fish habitat selection, and there are potentially important factors that were not included in our analysis. Given that the hydrodynamic habitat model output is extremely sensitive to model formulation, researchers, in essence, let the fish make the decision on which parameters were important. This model selection framework is likely the most robust method to achieving model parsimony and is a step towards a more 'holistic' approach of fish habitat selection.

## CHAPTER 5: Conclusions and Recommendations

Researchers developed and applied a series of habitat suitability models to juvenile Chinook salmon and steelhead trout in the American River and Mokelumne. Through combining extensive surveys and mapping with previous modeling efforts, researchers sought to develop and apply quantitative methods to identify and quantify suitable salmonid habitat. This project was motivated in part by the difficult management decisions that are associated with the management of these imperiled salmonids in these highly modified rivers. For example, during the extensive snorkel surveys juvenile salmonids were observed at extremely low densities (between 0.000858 and 0.00447 fish m<sup>-2</sup>, depending on the river, species). These low densities highlight the population status of salmonids in these systems and indicate the importance of this and other projects.

Mapping out suitable habitat provided key visualization of the location of suitable habitat for juvenile salmon across different flow regimes. The location of suitable habitat was variable, but often was identified as margin habitat or on riverine features such as gravel bars or at the head or tails of islands. Preferred habitat for steelhead and Chinook salmon appeared to be similar and often overlapping. In both river, studies focused on reaches that had side channels constructed in previous restoration engineering projects. The American River side channel was not identified as high quality habitat in most model formulations; there was some habitat associated with the margins of the channel, but the majority of the channel was not predicted to be preferred by juvenile salmonids. In contrast, the Mokelumne side channel was predicted to be excellent fish habitat at higher discharges. However, at low discharge (200 cfs) the side channel did not have flow through it, obviously rendering it unsuitable salmonid habitat. These visualizations highlight the dynamic nature of salmon habitat. Different habitats will be suitable at different discharges, more of the river channel will be inundated but there will be often higher velocities in the main channel habitat. Channel morphology will define these interactions between discharge and salmon habitat. In these highly controlled systems, where dam operators control river flows and restoration engineers change the river morphology, collaboration between these groups will help facilitate the management of these systems. For example, side channels should be engineered with explicit consideration of the future flow regime.

Hydrodynamic habitat model predictions were extremely sensitive to model formulation. The inclusion of different factors such as substrate versus cover often drove fairly substantial differences in the location of predicted suitable habitat. In addition, different model formulations drove substantial differences in the amount of habitat (the weighted usable area). Different model formulations led to different quantitative and qualitative relationships between discharge and WUA. The decision to include cover as a factor in the model controlled whether increased discharge led to increasing or decreasing salmonid habitat. These results should be strong evidence that care should be taken before making important decisions based on output from a single model formulation.

How do we move beyond the relatively arbitrary decision on what factors to include in models? Using a model selection framework such as the one performed, where a series of competing models are compared to the observed characteristics of inhabited and uninhabited locations is

recommended. In essence, let the fish identify which model to use. The factors that were consistently important were velocity, depth, adjacent velocity, and temperature. While the first three factors are generally included in models, water temperature is only rarely included in models such as this. A bioenergetics suitability curve was developed that allowed predictions of the location of fish based on water temperature and food abundance. While it is intuitively obvious that temperature is important for cold water fish, researchers recommend the inclusion of temperature into habitat suitability models, especially for these salmonid species that are located toward the southern extent of their range. Fish habitat selection can be controlled by multiple factors, including factors that were not considered in the analyses. There is a need to not force past model assumptions on fish habitat selection, but rather let the fish directly inform the models, allowing for a more 'holistic' approach.

Management and conservation of salmonids in these highly modified systems is a deeply challenging problem, with strong conflicting pressures from multiple users. This project developed and applied a series of models that visualized and quantified salmonid habitat at different river discharges. These quantitative approaches provided insight into the fundamentally difficult topic of suitable fish habitat. The "best" fish habitat will be influenced by multiple factors that vary across space and time; fish habitat will be dynamic. While considerable advances have been made in the modeling approaches involved in quantifying and identifying salmonid habitat, the serious sensitivity of these models has also been demonstrated. Full realization of model uncertainty is imperative in order to use these models properly to inform management of these modified rivers.

## **GLOSSARY**

AIC Akaike Suitability Criteria

CSI Composite Suitability Criteria

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