UNITED STATES DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
NATIONAL MARINE FISHERIES SERVICE
WEST COAST REGION
650 Capitol Mall, Suite 5-100
Sacramento, California 95814-4706

August 27, 2020

In response refer to:
WF:WCR:FERC P-2299 / P-14581

Kimberly D. Bose, Secretary
Federal Energy Regulatory Commission
888 First Street, NE
Washington, D.C. 20426

Re: The U.S. Department of Commerce's, NOAA Fisheries, West Coast Region's Technical Assistance for the Federal Energy Regulatory Commission's Licensing of the Don Pedro (P-2299) and La Grange (P-14581) FERC Projects.

Dear Secretary Bose:

Pursuant to our responsibilities for managing Chinook salmon and steelhead in the Tuolumne River, the U.S. Department of Commerce, NOAA Fisheries, West Coast Region (NMFS), contracted for an independent third party review of the Turlock and Modesto Irrigation Districts' Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*) population models.

As technical assistance, NMFS is filing herein, the following Report in Enclosure A:
"*Third Party Review of Tuolumne River Chinook Salmon and Oncorhynchus mykiss Population Models*." Prepared by Anchor QEA, LLC, Seattle, WA for NMFS, West Coast Region, Sacramento, CA. August 13, 2020.

The report provides information regarding the details and critique of the two salmonid models used in the P-2299 and P-14581 proceedings. If you have questions about this report, please contact Mr. Tom Holley at (916) 930-5592.

Sincerely,

Steve Edmondson
FERC Branch Supervisor
NMFS, West Coast Region

Enclosures

cc: FERC Service List P-2299, P-14581

Enclosure A

UNITED STATES OF AMERICA
FEDERAL ENERGY REGULATORY COMMISSION

Turlock and Modesto Irrigation Districts	**)**	
La Grange Hydroelectric Project	**)**	**Project No. 14581**
New Don Pedro Hydroelectric Project	**)**	**Project No. 2299**
Tuolumne River	**)**	

NOAA'S NATIONAL MARINE FISHERIES SERVICE'S
TECHNICAL REVIEW OF SALMONID POPULATION MODELS
E-FILED TO THE FERC PROJECTS' DOCKETS ABOVE

"*Third Party Review of Tuolumne River Chinook Salmon and Oncorhynchus mykiss Population Models*." Prepared by Anchor QEA, LLC, Seattle, WA for NMFS, West Coast Region, Sacramento, CA. August 13, 2020.

Enclosure B

UNITED STATES OF AMERICA
FEDERAL ENERGY REGULATORY COMMISSION

Turlock and Modesto Irrigation Districts	)	
La Grange Hydroelectric Project	)	**Project No. 14581**
New Don Pedro Hydroelectric Project	)	**Project No. 2299**
Tuolumne River	)	

CERTIFICATE OF SERVICE

I hereby certify that I have this day served, by first class mail or electronic mail, a letter to Secretary Bose of the Federal Energy Regulatory Commission (FERC), the U.S. Department of Commerce's, National Oceanic and Atmospheric Administration's, National Marine Fisheries Service's Report: "*Third Party Review of Tuolumne River Chinook Salmon and Oncorhynchus mykiss Population Models*," for the above-captioned proceedings, and this Certificate of Service upon each person designated on the official service lists compiled by the FERC in the above-captioned proceedings.

Dated this 27th day of August 2020

William E. Foster
National Marine Fisheries Service

August 2020
Tuolumne Model Review

ANCHOR QEA

Third Party Review of Tuolumne River Chinook Salmon and *Oncorhynchus mykiss* Population Models

California Central Valley Office
West Coast Region
NOAA Fisheries

Final Report

August 2020
Tuolumne Model Review

Third Party Review of Tuolumne River Chinook Salmon and *Oncorhynchus mykiss* Population Models

Prepared for
NOAA Fisheries
California Central Valley Office
650 Capitol Mall, Suite 5-100
Sacramento, CA 95814

Prepared by
Anchor QEA, LLC
1201 3rd Avenue, Suite 2600
Seattle, WA 98101

Project Number: 190912-02.01
Final Report

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ABBREVIATIONS

af	acre feet
CCSF	City and County of San Francisco
CCV	California's Central Valley
CDFW	California Department of Fish and Wildlife
cfs	cubic feet per second
Districts	Turlock Irrigation District and Modesto Irrigation District
DNA	deoxyribonucleic acid
DPS	Distinct Population Segment
ESA	Endangered Species Act
ESU	Evolutionarily Significant Unit
FERC	Federal Energy Regulatory Commission
GLM	general linear model
MID	Modesto Irrigation District
mm	millimeters
MWAT	maximum weekly (7-day) average temperature
NOAA	National Oceanic and Atmospheric Administration
PIT	passive integrated transponder
Reclamation	U.S. Bureau of Reclamation
review team	Anchor QEA Review Team
RM	river mile
RST	rotary screw trap
SAR	smolt-to-adult recruit survival
S-R	stock-recruitment
TID	Turlock Irrigation District
TRTAC	Tuolumne River Technical Advisory Committee
USGS	U.S. Geological Survey
VSP	Viable Salmonid Population
WUA	weighted usable area
WY	water year
YOY	young-of-year

Executive Summary

This report provides an independent review of the Chinook salmon (*Oncorhynchus tshawytscha*) and *O. mykiss* population models developed by the Turlock Irrigation District and Modesto Irrigation District (collectively we refer to these as "the Districts"). The models were designed to assess the extent to which the abundance of Chinook salmon and *O. mykiss* in the Tuolumne River may be affected by in-river factors, identify factors that influence life-stage specific production and critical life stages, and compare relative changes in smolt population size and smolt productivity between potential alternative management scenarios. The review team consisted of five scientists with expertise in salmonid ecology, population dynamics, modeling, hydrology and engineering, geomorphology, sediment dynamics, and habitat restoration. Each member of the review team has over 35 years of professional experience.

We evaluated the models and supporting documents to determine if the models are usable and useful. That is, from our perspective, can the models be used to identify critical life stages, identify and evaluate life-stage-specific limiting factors, and compare relative changes in smolt population abundance and smolt productivity among alternative management scenarios? Given the large amount of information collected as part of the project, the models are used to help synthesize and distill the information into results that can be used to evaluate management scenarios. However, it is important to point out that all models make simplifying assumptions. This ensures that to a certain degree all models are ultimately wrong or at least incomplete. We viewed the models in this context. Our goal in this review was to determine if the models, their assumptions, and the data used to populate the models are adequate enough to make them useful tools for evaluating management scenarios, and whether they were designed in a such manner that they can be easily used by the Districts and stakeholders.

Our review was straightforward and included reviewing model and data reports prepared by the Districts along with scientific information from California's Central Valley and other regions. As part of our review, we considered how the Districts incorporated the Viable Salmonid Population concept developed by National Oceanic and Atmospheric Administration (NOAA) Fisheries to define the essential characteristics of a viable salmon population. The concept is used in recovery planning for populations listed as threatened or endangered under the Endangered Species Act (ESA), with a focus on abundance, intrinsic productivity, and biological diversity. We also found it helpful to consider both the inputs and outputs of the Tuolumne population models within a conventional stock-recruitment model. With considerable effort, we were able to evaluate model coding and run the models under different spawner escapement levels and assumed smolt-to-adult return rates to understand modeled relationships. To improve the quality of our review, we submitted a letter requesting additional information and clarification regarding the models (Appendix A). Their responses helped us in our review of the models and we greatly appreciated the quick response from

the Districts and their consultants to our request (Appendix A). Finally, most members of the review team toured the lower Tuolumne River in January 2020 to gain a perspective of the Tuolumne River that is not available from reports.

Based on our review of the models, the supporting information, and other pertinent information, we conclude the following: 1) the three physical models developed to support the population models are useful and usable; 2) the Chinook salmon population model is useful but not usable by all stakeholders; and 3) the *O. mykiss* population model is neither useful nor usable. Below, we summarize our reasons for these findings.

Physical Models

We found no significant issues with the three physical models that support the population models. The Tuolumne River Operations Model represents observed operations relatively well; however, we recommend that an operations model with more capability and flexibility be used in the future, such as the RiverWare model that is commonly used by the U.S. Bureau of Reclamation for operational planning in complex river basins. The Don Pedro Reservoir Temperature Model results appear adequate for use in the Lower Tuolumne River Temperature Model, and the Lower Tuolumne River Temperature Model predictions are likely satisfactory for use in fish population modeling. We noted that the Lower Tuolumne River Temperature Model was not able to represent diurnal fluctuations accurately in some reaches of the river. This is likely due to unknown groundwater inflows or outflows and the presence of the special run pools that may act as a thermal buffer due to the large volume of water in the pools. Because the population models use daily average temperatures, the predictions from the Lower Tuolumne River Temperature Model are likely satisfactory for use in fish population modeling.

Chinook Salmon Population Model

The Chinook salmon population model is a complex, spatially explicit, individual-based model that tracks each fish within the modeled population along the river on a daily basis. Importantly, it is not a full life-cycle model, meaning that it makes no attempt to complete the life cycle of the surviving smolts. Therefore, it cannot predict equilibrium spawner abundance levels that would be expected to occur under a prescribed set of management actions. The model is written in the "R" statistical software package and we initially found it difficult to run, track, and alter different aspects of the inputs. The modeling reports were not helpful in this regard. Once we became familiar with the model, it was easier to operate. We doubt that many stakeholders will find the model usable. From our perspective, given that this is the river, fish conservation, and fisheries management tool that will be used for the term of the Federal Energy Regulatory Commission (FERC) license, the Districts should make the Chinook salmon population model available to stakeholders if they have not already done so, and the stakeholders need to learn how to operate and use the model to assess tradeoffs between flow alternatives. Model users would benefit by having the model developers incorporate model features to make it easier to evaluate customized water management scenarios such as a user-friendly interface like Shiny (an R package for developing interactive web applications).

We found the Chinook salmon population model to be a useful tool for evaluating the production of emigrant Chinook salmon smolts in the Tuolumne River in relation to habitat conditions, including flow regimes and predation effects. The model can provide important insights to scientists and managers alike about the status of the population and factors affecting population performance. More specifically, we found that it appears to have utility to help diagnose the effects of various conditions threatening population performance and identify and evaluate management actions that can improve performance. That said, there are several areas in which the model can be improved. In addition, reports prepared by the Districts and their consultants do not clearly present all the results from the model. Below, we summarize a few important findings and issues we identified during our review of the Chinook salmon population model (more detailed comments are provided in the body of the report).

- We conclude that the model indicates that the Chinook salmon population is most threatened by extremely low intrinsic productivity. This means that the population is being most adversely affected by habitat quality (not quantity), which would include the effects of predator populations. According to the model, a shortage of habitat quantity, including spawning habitat and gravel availability, is not a limitation on the population at abundance levels that are of concern. Thus, gravel augmentation would not significantly improve population performance. Similarly, increasing flow during spawning to increase available spawning habitat would likely have only small or negligible effects on the population.
- The model, as configured, indicates that the status of the Chinook salmon population is extremely precarious and bold actions will be needed to prevent extirpation. This need, according to the model, would best be met by very substantial increases in flow releases during spring (the period of active smolt outmigration from the river). The model suggests that management actions with the most certainty in providing real benefits would involve increases in flows during smolt outmigration. Other actions would be expected to provide relatively low benefits compared to spring flow increases. These include reductions in predation rates (unless those reductions could be of a significant magnitude) and increases in spawning habitat through gravel augmentation (even if those increases were large).
- The model is not a full life cycle, which hampers its utility for evaluating potential benefits of management actions to the overall population. The model also does not account for population components that contribute to overall adult production other than fish that smolt while in the river. Fry migrants (newly emerged fry), slightly older fry emigrants, juveniles that emigrant prior to smolting, and juveniles that residualize and continue to rear in the river are treated as mortalities in terms of their contribution to population productivity. In this regard,

the model has a very narrow scope that omits important life histories that are known to contribute to the population based on analysis of otoliths. While the model can be used to inform relative differences between management alternatives without including these life history expressions, the assessment will be incomplete without considering how the entire population responds to the actions. Thus, in our view, the model falls short of meeting the guidance provided by FERC on model development. Because it is not a full life-cycle model, the Chinook salmon population model as configured is inadequate for managing the Chinook salmon population for conservation or fisheries over the term of a FERC license because it does not inform surplus over replacement, as discussed in the body of this report. It is an in-river smolt production model that estimates the smolt production resulting from a pre-set number of spawners.

- Uncertainties exist with the model, particularly with regard to parameters related to predation effects. Estimates of mortality during the smolt-to-smolt life stage based on the rotary screw trap (RST) studies are the largest driver of the results produced from the model. Smolt-to-smolt mortality refers to the loss of fish in the river from the point of attaining smolt status to the point of leaving the river as an emigrant. We found the model did not calibrate well to observed smolts arriving at the Waterford RST, which brings into question its ability to estimate life-stage transitions and survival to this sampling location. The relationship between flow and survival based on the RST data can take several forms, all of which appeared to incorporate a high degree of variability in the data at certain flow levels. We believe there is a need to improve the estimates of smolt-to-smolt survival if the model is to be used for evaluating management alternatives, or at the very least, to improve the confidence in the estimates and the relationships between survival and flow developed based on the estimates.
- The volume of water available for fish conservation and fisheries management is limited. Given this, stakeholders should use the model to explore tradeoffs among 1) winter flow augmentation to displace fry downstream (knowing that displaced fry in the model do not contribute to smolt-to-smolt survival but some do return as adults); 2) winter flow augmentation for rearing (early rearing flows during March and possibly February have been found to be particularly important factors controlling adult recruitment in the San Joaquin River Basin); 3) spring pulse flows during April and May as proposed by the Districts; and 4) the value of fall pulse flows for adult attraction.
- We estimated the number of adult recruits that would be produced from the modeled estimates of smolt emigrants leaving the Tuolumne River, and using an optimistic average smolt-to-adult recruit survival (SAR) of 5% for illustration, the estimated intrinsic productivity of Chinook salmon is 0.14, which is well below the spawner replacement level of 1. Therefore, if all assumptions in the Chinook salmon population model are correct, the model suggests that the population has already been extirpated or will be soon. The situation is likely worse

than indicated by the model because harvest is not incorporated into the model nor is the effect of hatchery strays on reproductive success, and because an assumed SAR of 5% is unrealistically high.

- It is quite likely that predation is the reason for the apparent poor smolt-to-smolt survival. Therefore, it is reasonable to try and reduce predation effects during the smolt migration period. While predation effects are estimated to be large, the Chinook salmon production model cannot identify the number of predators that would need to be removed or how much of a reduction in consumption would be required to achieve a significant increase in smolt-to-smolt survival. The response from predator control is assumed, not predicted. In contrast, the model predicts, and does not assume, changes in smolt-to-smolt survival associated with flow. That is, the model demonstrates a clear and positive relationship between mean April flows and smolt-to-smolt survival in the Tuolumne River.
- A modeling report needs to be prepared that provides greater clarity and transparency for how the model is structured and operated with clear and concise instructions for application. Modeling results need to be presented in a manner that provides clear guidance on interpreting model outputs for application to management. These aspects should be developed in collaboration with stakeholders and potential users.

O. mykiss Population Model

The *O. mykiss* population model is a complex, spatially explicit, individual-based model. It uses an individual-based framework to represent the major life history processes affecting *O. mykiss* maturation, spawning, egg incubation, juvenile growth, movement, mortality, and anadromy rates to estimate juvenile and smolt production and end-of-year age-2 and older fish (assumed to reflect adult abundance) as a function of varying flows and water temperatures in the lower Tuolumne River. As with the Chinook salmon population model, the *O. mykiss* population model is not usable by most stakeholders. In addition, the *O. mykiss* modeling report is confusing and difficult to follow given the complexity of the model. It took us a large amount of time to become competent enough to run and understand the model. It is not user-friendly, which means that few will be able to run and understand the model results. This is unfortunate in that regulatory agencies probably cannot use the model to evaluate various management strategies. As with the Chinook salmon population model, a user-friendly interface is needed to make the model more useful to all stakeholders for modeling scenarios other than those packaged with the model.

Unlike the Chinook salmon population model, after our review and analysis of the *O. mykiss* population model, we conclude that the *O. mykiss* population model is not useful at this time. Although it is evident that the investigators did a large amount of work in developing the model, we found that the structure and conceptual underpinnings of the *O. mykiss* population model are not well supported for this species in the Tuolumne River. Because of very limited data for *O. mykiss* in the river, and particularly with regard to the possibilities for anadromy, and the obvious adaptation of the model from the Chinook salmon model including its parameterization, the *O. mykiss* model seems contrived with questionable utility. Perhaps most confusing to us is the use of a combination of a part of the steelhead life history together with a resident population, which also does not incorporate a full life cycle. The outputs from this mixture are difficult to interpret and apply. Below, we summarize a few important concerns we have with the *O. mykiss* population model (more detailed comments are provided in the body of the report).

- The *O. mykiss* population model should not be used for diagnosing or evaluating management actions related to the anadromous form of this species, given the model's current structure, its parameterization, and its calibration and validation.
- The model attempts to combine an artificial and unrealistic number of steelhead spawners with two different levels of resident fish spawners in a manner that is unnatural, not transparent, and difficult to follow in both the model and the model documentation. The conceptual underpinnings of doing this in the model are not well supported. We found several significant inconsistencies between the original and updated modeling results that are difficult to understand, which raised further concerns to us about the reliability of the model.
- The model is structured and parameterized based on concepts and parameter settings used in the Chinook salmon model. The life histories and behaviors of these two species are dramatically different. A model structured to accommodate juvenile Chinook salmon is inappropriate to address the needs for *O. mykiss* modeling, especially for the anadromous form. Movement patterns of fry and juveniles of ocean-type Chinook salmon are much different than those of juvenile *O. mykiss*, whether in the anadromous or resident form. Models developed to assess responses of these two species to freshwater environmental factors, therefore, need to account for differences in life history patterns between the species in how each individual model is structured and parameterized.
- A key assumption in the *O. mykiss* model is that predation by predatory fishes is a major cause of poor performance of *O. mykiss*, and presumably to the production of the anadromous form of the species. Three parameters within the model were informed by the results of the RST data as it was used to estimate smolt-to-smolt survival of Chinook salmon. However, there is no evidence that predation on *O. mykiss* is comparable to or similar in any way to that of juvenile Chinook salmon. In fact, as far as we can tell, there is no evidence of predation on juvenile *O. mykiss* by predatory fishes in the Tuolumne River.
- Because of limited amounts of information available for *O. mykiss* in the river, the model cannot be adequately calibrated or validated. The authors of the *O. mykiss* modeling report recognized this limitation. They stated: "In the absence of reliable information on the numbers and timing of any anadromous *O. mykiss* spawning and the factors contributing to anadromy in the Tuolumne River, the relative changes in the production of *O. mykiss* smolts resulting

from different flow and temperature conditions within the Tuolumne River cannot be reliably assessed using the TROm model." We agree with this assessment.

- We found that the factors affecting anadromy of *O. mykiss* in the Tuolumne River were not adequately addressed. It would be more useful to apply a framework like the one described by Satterthwaite et al. (2009, 2010) to *O. mykiss* in the Tuolumne River to examine potential anadromy because it is the anadromous form of the species that is listed under ESA, not the resident form.

Despite these shortcomings, it bears noting that the model, as developed, found water temperatures to be the major environmental factor driving juvenile *O. mykiss* productivity downstream of the dam. Flows released below La Grange Dam are apparently the major factor affecting water temperatures.

Recommendations

We concluded that the Chinook salmon population model is useful but not usable by all stakeholders and the *O. mykiss* population model is neither useful nor usable. From our perspective, solutions exist for the issues we raised with the models. Based on our review and analyses of the population models, we offer the recommendations listed below to gather additional information and conduct additional analyses to increase confidence with the models, characterize scientific uncertainty, and address key aspects of managing the river over the term of the FERC license that are missing from the current analytical framework. For the *O. mykiss* population model, we offer a suggested path forward focused on understanding how to stimulate anadromy and what that implies in terms of water management and project operations. However, from our perspective, even if the *O. mykiss* model in its present configuration could be improved to address the shortcomings we identified, it is a rainbow trout model that is not useful to NOAA Fisheries as a steelhead recovery tool. Implementing these recommendations will improve the understanding of key relationships between the species modeled and their environment and analyses of alternatives designed to improve salmonid productivity in the lower Tuolumne River.

- For both species:
  - Develop an analytical framework that will allow an evaluation of both target species at the same time. Currently, each species is addressed separately. We found no discussion of optimizing management alternatives for both species at the same time or identifying tradeoffs between species and alternatives. A key attribute of quantitative models is that they support these types of analyses and discussions.
  - Incorporate climate change into the modeling framework for both species to assess the potential effects changes in hydrology and water temperatures will have on river management alternatives and salmon and steelhead populations over the course of the FERC license.

- For Chinook salmon:
  - Characterize the variability in modeled flow-to-survival relationships to inform the sensitivity of model outputs to key relationships and data points incorporated into the model. Estimating uncertainty is a critical element of communicating model results.
  - Conduct additional analysis of Tuolumne River RST data because it appears that multiple factors associated with fry and smolt catch are interacting (e.g., absolute catch, flow, and rearing and behavior). These factors influence estimated catch and survival between RSTs, and thus the number of smolts estimated to be emigrating from the Tuolumne River. The influence of these factors on the magnitude and variability of smolt production should to be addressed in an analytical framework, including the influence and sensitivity of RST catch during periods of ascending flow that were not incorporated into the Chinook salmon smolt flow-to-survival relationship used in the population model.
  - Estimate survival using mark-recapture methods that incorporate estimated detection probability into survival estimates to independently validate RST-based estimates and inform flow-to-survival relationships. Conduct the studies over multiple years and under all major flow conditions (water year types) and within each year and across reaches. This is needed to develop a better understanding of how survival varies with multiple environmental factors and location.
  - Incorporate the effects of hatchery strays on the overall productivity of the population into the Chinook salmon model. Based on our analysis, Chinook salmon in the Tuolumne River may already be close to being extirpated—the population appears to be precarious at best. The effects of hatchery strays on the overall productivity of the population were not incorporated into the Chinook salmon population model. This needs to be included to inform whether river management alternatives can reduce the negative impact of strays on the natural population and increase population productivity.
  - Conduct additional Chinook salmon otolith analyses to quantify stray rates, reconstruct the in-river conditions conducive to juvenile survival and adult escapement, and inform water management alternatives.
  - Conduct a detailed study of parentage from deoxyribonucleic acid (DNA) to help inform the effects of redd superimposition on Chinook salmon egg-to-fry survival.
- For *O. mykiss*:
  - Model growth as a function of environmental conditions and use sensitivity analyses to predict likely evolutionary endpoints to assess how best to express anadromy in the Tuolumne River and what that implies in terms of water management and project operations. With that information in hand, implications and tradeoffs between

management goals for Chinook salmon and steelhead and recovery goals for steelhead can be discussed and decisions made on the best operations and water management scenarios for both species.

- Consider recruitment from "outside" sources in the model because the influence of increased flow effects in the lower Tuolumne River cannot be separated from effects on estimated population size due to recruitment from above La Grange Dam in high-flow years such as 2011.
- Conduct a detailed study of parentage from DNA to help inform the effects of redd superimposition on *O. mykiss* egg-to-fry survival.

Acknowledgements

Finally, we want to acknowledge the tremendous amount of work and effort conducted by the Districts, their consultants, and the stakeholders to gather the information needed to parameterize and develop the models. Although we found faults with both population models and concluded that the *O. mykiss* population model is not currently useful, we believe the investigators did their best to develop models with the available information. We also thank NOAA Fisheries for giving us the opportunity to review the models. We hope the Districts and stakeholders find our independent review helpful and constructive.

1 Introduction

This report summarizes an independent review of the Chinook salmon (*Oncorhynchus tshawytscha*) and *O. mykiss* population models developed by the Turlock Irrigation District (TID) and Modesto Irrigation District (MID) (collectively we refer to these as "the Districts") to assess the extent to which the abundance of Chinook salmon and *O. mykiss* in the Tuolumne River may be affected by in-river factors. The models were designed and parameterized to investigate the influences of various factors on the life-stage specific production of both species, identify critical life stages that are particularly adversely affected by those factors, and compare relative changes in population size between potential alternative management scenarios (Stillwater Sciences 2017a,b). The Anchor QEA Review Team (review team) consisted of the following individuals:

- **Kathy Vanderwal Dubé**: Kathy is a geomorphologist and owner of Watershed GeoDynamics (Homer, Alaska). Kathy received an MS, Geological Sciences, in 1985 from the University of Washington and a BS, Environmental Sciences & Resource Management, in 1982 from Lehigh University. Kathy specializes in erosion, sediment transport, instream large wood, and aquatic habitat evaluations. Her work has ranged from evaluating rivers in pristine environments to highly managed systems. Her work integrates a variety of tools including field work; analysis of historical maps, aerial photographs, and LiDAR; GIS; and sediment transport modeling. Her role on the review team focused on the historical and contemporary geomorphic setting of the Tuolumne River, floodplain activation, spawning gravel limitations, and flow-habitat analysis using PHABSIM.
- **John Ferguson**: John is a Principal Fisheries Scientist with Anchor QEA (Seattle, Washington). John received a PhD, Biology, Swedish University of Agricultural Sciences, in 2008; an MS, Aquatic Ecology, University of California, Davis, in 1976; and a BS, Fish and Wildlife Biology, University of California, Davis, in 1974. His work focuses on evaluating the behavior and survival of salmon in large river systems and applying this information to water management decisions. His role on the review team included project management; review of rotary screw trap (RST), predation, and Chinook salmon survival data; and assessment of the architecture and parametrization of the two population models.
- **Tracy Hillman**: Tracy is a Senior Ecologist at BioAnalysts, Inc (Boise, Idaho). Tracy received a PhD, Ecology, Idaho State University, in 1991; an MS, Ecology/Zoology, Idaho State University, in 1987; and a BS, Biology, Montana State University, in 1984. Tracy is an expert in monitoring, hatchery evaluations, fish and habitat sampling, population dynamics, experimental design and statistical analysis, and animal behavior. His role on the review team included assessing the flow-habitat analysis using PHABSIM, spawning gravel limitations, and redd superimposition.
- **Larry Lestelle**: Larry is a Senior Biologist and owner of Biostream Environmental (Poulsbo, Washington). Larry received an MS, Fisheries Science, University of Washington, in 1978 and a

BS, Fisheries Science, University of Washington, in 1972. Larry is an expert in a wide variety of issues related to fish population dynamics and modeling, salmonid ecology, resource assessment and enhancement, fisheries management, and environmental impacts. He has developed a variety of models employed in assessments of salmon population performance, diagnosing limiting factors, and the development of salmon recovery and restoration plans. Larry was a lead architect of the Ecosystem Diagnosis and Treatment Model. His role on the review team focused on assessing model architecture and parameterization.

- **Bob Montgomery**: Bob is a Principal Water Resource Engineer with Anchor QEA (Seattle, Washington). Bob received an MS, Civil Engineering, University of Washington, in 1984; a BS, Civil Engineering, University of Washington, in 1979; and was a Valle Scholar at the Royal Institute of Technology, Stockholm, Sweden, in 1983 to 1984. Bob has led hydrologic, water management studies, flow, and habitat restoration projects on many managed river systems in the western United States. Recent project experience includes hydrologic, hydraulic, geomorphic, and other engineering studies as well as habitat restoration studies on the Chehalis River as part of the Chehalis Basin Strategy; leading the technical studies for the Yakima River Basin Integrated Water Resources Management Plan; and managing a large on-call fisheries restoration contract for the U.S. Bureau of Reclamation (Reclamation). His role on the review team focused on assessing the physical models (operations, reservoir temperature, river, and floodplain hydraulic assessment), where the output from these physical models was used as input into the population models.

The models were reviewed from several perspectives. First, we based our review on language provided by Federal Energy Regulatory Commission (FERC) staff to the Districts in Element No.1 of the Study Plan Determinations for both the Chinook Salmon Population Model Study (W&AR-06) and the *O. mykiss* Population Study (W&AR-10). This guidance stated the population models should include mechanisms and parameters "that address the association between flows, water temperature, changing habitat conditions, predation, and the population response for specific in-river life-stages including smolts for existing conditions and for potential future conditions" (Stillwater Sciences 2017a,b). Accordingly, we judged the efficacy of the models as to how accurately they capture and simulate how the different life stages contribute to population-level responses to flow, temperature, habitat, and predation under contemporary and future conditions.

Second, our review makes clear that other models have been developed to assess how management of the Tuolumne River affects Chinook salmon productivity.[1] For example, Stillwater Sciences (2017a)

[1] The word productivity has various meanings in biological and fish population dynamics literature. It is critical for understanding the Stillwater Sciences reports and this report that the definitions used in these documents is made clear because the word is used in very different ways among these reports. The Stillwater Sciences reports use the term as the measure of relative reproductive success expressed as the smolts resulting from a pre-set number of spawners, i.e., smolts per female spawner.. As explained in this report, another meaning often used in population dynamics literature (e.g., Hilborn and Walters 1992) refers to intrinsic productivity, which is the number of progeny per parent spawner produced at very low spawner density (or in the absence of any

states that estimates of outmigration survival in recent RST reports (2008 to 2012) are well below that suggested by the Tuolumne River Technical Advisory Committee (TRTAC) smolt survival relationship. Also, Mesick and Marsten (2007) developed a relationship between the number of smolt-sized Chinook salmon outmigrants passing the Grayson RST site (river mile [RM] 5) and flow at La Grange between March 1 and June 15 from 1998 to 2006. The relationships developed by TRTAC and Mesick and Marsten (2007) are models, albeit much simpler models than those reviewed here, that are hypotheses regarding how the lower Tuolumne River and its management influence Chinook salmon productivity. These alternative models or hypotheses were not incorporated into the Chinook salmon population model to assess the sensitivity of model results to underlying assumptions and hypothesized relationships. During our review we found no alternative models or hypotheses presented in the Chinook salmon and *O. mykiss* population model outputs. Therefore, we assumed that fish conservation and fisheries management of the lower Tuolumne River over the term of the FERC license is being based on the models being reviewed, and we reviewed them in this context.

Lastly, information on estimated productivity based on the models was provided in a letter from the Districts (TID and MID) to FERC dated December 11, 2019 (TID/MID 2019). The letter provided results on individual alternatives and combinations of proposed alternatives for both species. The letter was highly informative and provided insights into what the models produced and their sensitivity to different parameters and alternatives. Our conclusions were not based on the results identified in TID/MID (2019). However, the letter provided a lens through which we viewed the models, and it was therefore part of the approach taken in this review. Based on TID/MID (2019), the following initial observations were made regarding Chinook salmon productivity:

- The metric chosen to report changes in productivity is smolts per female spawner, not total smolts, parr, or fry produced. Note that productivity in the Stillwater Sciences report is not intrinsic productivity because it incorporates effects of population density into the metric (see Section 2.4 for a discussion of terms).
- Estimated smolts per female spawner produced by the model is extremely low and ranges from 6.25 to 16.50. The relative changes among alternatives presented in Table 2.3-2 (TID/MID 2019) represent mathematical differences that struck us as being biologically meaningless. This is because the values presented are not close to the 200 smolts per female spawner that would have to be produced for the population to be at replacement given an assumed 1% smolt-to-adult return rate, and above that level for the population to increase.
- The results of estimated smolts per female spawner suggest that either the model is correct and Chinook salmon productivity is extremely low and the species is functionally extirpated (or will be shortly), or the model is not capturing some components of production (because

density-dependence). The reader needs to be aware that the scientific literature does not always distinguish the difference in meaning of these two different applications. The terms applying both meanings have application in this report, but we are careful to distinguish which meaning is intended. See Section 2.4 for discussion on this matter.

based on annual escapement estimates fish appear to continue to be produced and return to the river, especially under wet hydrological conditions, though this may be confounded due to the presence of hatchery strays).

- The model appeared insensitive to flow effects because the "TBI [The Bay Institute] alternative" produced 9.31 smolts per female spawner with a flow volume of 854 thousand acre feet (af), whereas the "base case" produced 6.25 smolts per female spawner with a flow volume of 216 thousand af; therefore, a 400% increase in flow resulted in a small numerical change in productivity and an insignificant improvement in biological productivity.
- The non-flow alternatives showed the greatest increase in productivity with the "VA [Voluntary Agreement] with all proposed non-flow measures" alternative showing the highest value (16.5 smolts per female spawner).
- These patterns among alternatives were similar between model runs with 2,000 spawners and 10,000 spawners.
- Within each alternative modeled, productivity decreased at 10,000 spawners compared to 2,000 spawners, suggesting a density-dependent effect.
- Productivity values for alternatives are presented to two decimal places; this implies precision in the model outputs that is inappropriate given the numerous assumptions. Presenting smolts to the level of 0.01 fish is not meaningful biologically given the overall low number of smolts produced by the system, as discussed above.
- The point estimates of productivity lack any associated variance, making it difficult to judge whether estimated productivity among alternatives is truly different.
- The Chinook salmon population spawning in the river appears to be a demographic sink (Johnson et al. 2012).

Based on TID/MID (2019), the following initial observations were made regarding *O. mykiss* productivity:

- The metric chosen to report changes in productivity is young-of-year (YOY) juveniles under low and high spawner density, not smolts per female spawner or total smolts produced, even though the guidance language from FERC described above specifically mentioned population responses for smolts.
- Adult replacement rates were also estimated; in general, the values presented for all alternatives were around 1 and were similar under both low and high density. The exceptions were the "base case" and "interim flows" alternatives that produced lower adult replacement rates.
- Patterns in productivity among alternatives indicated largest increases in YOY produced were associated with the "VA flows with gravel augmentation," "VA with gravel cleaning," and "VA with all proposed non-flow measures" alternatives.
- The "TBI alternative" resulted in a 9% decrease in the number of YOY produced.

During our review, the Districts issued a letter to FERC regarding a coding error in the models that affects the allocation of juvenile fish between the floodplain and the main channel (TID/MID 2020c). According to this letter, correcting the code resulted in small positive changes in Chinook salmon smolt productivity among scenarios and no substantive changes in *O. mykiss* model results. The revised model outputs were reviewed and had no effect on our model interpretations or conclusions.

The methods employed in the review were straightforward. We conducted background reading of key model and data reports and then toured the lower Tuolumne River on January 16 and 17, 2020. River flow during the tour was approximately 400 cfs (U.S. Geological Survey [USGS] Gage 11289650, Tuolumne River at La Grange, California). The tour was organized and conducted by Stacie Smith and Thomas Holly from National Oceanic and Atmospheric Administration (NOAA) Fisheries and included support from Gretchen Murphy and Steve Tsao from California Department of Fish and Wildlife (CDFW). Following the tour, team members worked independently on model components based on their expertise described above. We reviewed model coding and ran both models under different spawner escapement levels and assumed smolt-to-adult return rates to understand modeled relationships. The review team conducted bi-weekly coordination calls to discuss information and findings. In May 2020, a letter was sent to Steve Edmundson (NOAA Fisheries) requesting additional information and clarifications regarding the population models (Appendix A). In July we received a response to this letter in the form of a Technical Memorandum from Stillwater Sciences to Michael Cooke, Turlock Irrigation District (Appendix A). The response letter confirmed and clarified our interpretations of how the models are structured, which we incorporated into our review. We greatly appreciate the time Stillwater Sciences spent developing their Technical Memorandum.

Finally, it is important to acknowledge that the Districts, their contractors and investigators, and stakeholders conducted a tremendous amount of work over several decades that focused on collecting and analyzing information needed to inform the status and trends of Chinook salmon and *O. mykiss* in the lower Tuolumne River. Relicensing participants participated in workshops held on January 17, 2012, and April 2, 2012, to review, discuss, and synthesize the available information. This resulted in the development of the Salmonid Population Information Integration and Synthesis Study Report (Stillwater Sciences 2013a) that was most helpful to us as reviewers. It has been a tremendous pleasure to review models that were developed based on such a rich source of diverse data.

2 Background

The historical setting of the Tuolumne River provides important context when reviewing the current performance of the fish populations as estimated by the population models. We briefly review the historical and contemporary setting below.

2.1 Biological Setting

Salmonid populations in the San Joaquin River basin were once some of the largest in the Central Valley (CDFG 1990). Historically, the river and its tributaries supported spring and fall Chinook salmon and steelhead (Yoshiyama et al. 2001; Moyle 2002). It can be concluded that historical distributions of anadromous salmonids in the Tuolumne River extended upstream from present-day New Don Pedro Dam. For salmon this is based on Yoshiyama et al. (1996), who documented the extent of anadromy in the upper watershed for spring and fall Chinook salmon. *O. mykiss* also ascended into the upper Tuolumne River because most extant populations today have retained their largely indigenous ancestry based on recent sampling of genetic variation (Pearse and Campbell 2018).

Extensive anthropogenic influences on Tuolumne River habitats since the Gold Rush resulted in significant declines in spring and fall Chinook salmon and steelhead populations (Stillwater Sciences 2013a). Historical counts of salmon and steelhead prior to the mid-1900s are unavailable. Because there are no spring Chinook salmon in the lower Tuolumne River, hereafter we refer to fall Chinook salmon as Chinook salmon.

The number of Chinook salmon returning to the Tuolumne River ranged from 100 to 45,900 fish between 1952 and 1970 (GrandTab escapement database maintained by CDFW, dated 20190507). Since the New Don Pedro Dam was completed in 1971, the estimated number of Chinook salmon returning to the Tuolumne River has ranged from 77 to 40,322 fish (GrandTab escapement database dated 20190507). Although the range in estimated escapement for both time periods (1952 to 1970 and after 1970) is generally similar, two important trends are apparent in the time series. First, peak escapement in the three periods of higher production since the early 1970s has declined from approximately 40,000 to 3,000 Chinook salmon. Second, the most recent cyclical increase in production of Chinook salmon in the San Joaquin River from 2011 to 2018 occurred to a greater degree in the Stanislaus and Mokelumne rivers compared to the Tuolumne River (Figure 1). Thus, during the contemporary period since 1971 the intrinsic productivity of Chinook salmon allowed the Tuolumne River population to greatly expand in abundance during cyclically favorable conditions, but this characteristic of population performance appears to have been reduced in the most recent time interval of peaks in abundance.

Figure 1
San Joaquin River tributaries Chinook salmon estimated escapement 1973 to 2019.

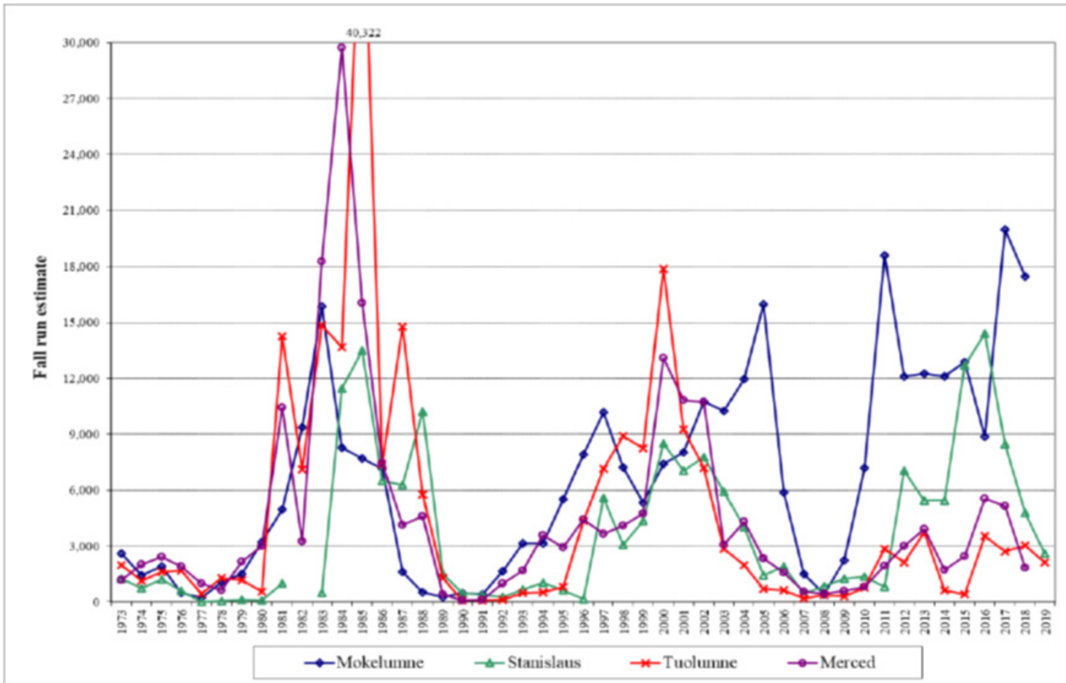


Exhibit 1B [2019 data for Mokelumne and Merced Rivers not available as of March 2020.]

Source: TID/MID 2020a.

There are no hatcheries located within the Tuolumne River basin. However, the rate at which hatchery-origin Chinook salmon stray into the Tuolumne River is high. Analysis of otoliths collected from unmarked Chinook salmon carcasses corresponding to outmigration years 1998, 1999, 2000, 2003, and 2009 indicated that 54% of the fish sampled were identified as wild and of Tuolumne River origin, 43% were identified as hatchery-origin, and 4% were identified as wild strays from other rivers (Stillwater Sciences 2016). For the most recent outmigration years analyzed (2003 and 2009), returning wild fish made up only 9% to 25% of the carcasses sampled, with large hatchery components originating from the Mokelumne River Hatchery in 2003 and the Coleman National Fish Hatchery in 2009 (Stillwater Sciences 2016). Starting in 2010, the CDFW has estimated the proportion of hatchery-origin Chinook salmon returning to the Tuolumne River each year based on recovery of coded wire tags from adipose clipped Chinook salmon sampled during spawning surveys. For 2014, the most recent year for which data are available, an estimated 65% of the Chinook salmon returning to the Tuolumne River were strays from hatcheries located in the Mokelumne, American, and Merced rivers (Palmer-Zwhalen et al. 2019). Our summary of coded wire tag data from CDFW annual reports including Palmer-Zwhalen et al. (2019) indicates the proportion of hatchery-origin Chinook salmon returning to the Tuolumne River averaged 50% during the 2010 to 2014 period. The implications of this phenomenon are discussed in Section 6.6.

For California Central Valley (CCV) steelhead, today, dams block access to 80% of the habitat that was historically available (Lindley et al. 2006). Declines in the abundance of salmon and steelhead in California resulted in the Central Valley (CV) spring-run Chinook salmon Evolutionarily Significant Unit (ESU) being listed as threatened under the Endangered Species Act (ESA) in 1999, and the Distinct Population Segment (DPS) of CCV steelhead being listed as threatened in 1998. The Tuolumne River downstream of La Grange Dam has been designated as critical habitat for CV spring-run Chinook salmon and CCV steelhead. The listing status for both species was unchanged following a status review in 2016.

A key recovery objective for both species is to secure existing populations by addressing stressors; also, CCV steelhead should be characterized as having two populations in the Southern Sierra Diversity Group at low risk of extinction (NMFS 2014). The two populations represent 2 of the 26 independent CCV steelhead populations that existed historically in this diversity group (NMFS 2014).

2.2 Physical Setting

The Tuolumne River originates on the west side of the Sierra Nevada mountains in Yosemite National Park and flows westerly for approximately 130 miles to its confluence with the San Joaquin River, west of the city of Modesto. The Tuolumne River drains 1,960 square miles and is the largest of three major tributaries to the San Joaquin River, with the other two being the Merced and the Stanislaus rivers. The watershed in the Sierra Nevada foothills is characterized by deep canyons, bedrock-lined river channels, and forested, mountainous terrain. Near the town of La Grange, the river flows out of the foothills through a gently sloping alluvial valley that is incised into Pleistocene alluvial fans, although there are several short sections where the channel is underlain or constrained by bedrock. The Tuolumne River is generally gravel-bedded upstream of the Geer Road Bridge at RM 24 and sand-bedded in the lower gradient reaches downstream from RM 24 (McBain and Trush 2004).

Runoff in the Tuolumne River basin is produced by rainfall and snowmelt. Rainfall runoff occurs primarily in the Sierra Nevada foothills and the valley floor between December and March. Runoff from the upper basin is produced by snowmelt that occurs primarily between April and July.

Human-induced changes to the Tuolumne River valley have profoundly affected both geomorphic and hydrologic characteristics of the river downstream from the Don Pedro Dam. In the following sections we describe the historical (pre-European settlement) conditions and contemporary conditions (the period since the New Don Pedro Dam was constructed in 1971).

2.2.1 Historical

Large-scale changes in natural flow patterns on the Tuolumne River began with construction of the original Don Pedro Reservoir (290,000 af storage capacity) and Hetch Hetchy Reservoir (206,000 af storage capacity) in the 1920s. The City and County of San Francisco (CCSF) began diverting waters from the Tuolumne River and Hetch Hetchy Reservoir in 1923. Hetch Hetchy Dam was raised in 1937 to increase storage capacity to 360,000 af. Lake Lloyd on Cherry Creek added another 268,000 af of storage in the basin in 1955. New Don Pedro Reservoir was constructed in 1971 with a storage capacity of 2.03 million af. Average annual unimpaired water yield for the Tuolumne River is approximately 1,900,000 af, with an estimated range from approximately 450,000 af to 4.6 million af (McBain and Trush 2000). Therefore, the total storage capacity in the basin exceeds the average annual natural runoff.

Prior to regulation and out-of-basin diversions, the natural flow hydrograph can be characterized as having components of fall storm pulses, winter and summer baseflows, winter floods, spring snowmelt floods and snowmelt recession, and transition periods between those components. Table 1 provides streamflow values by component and type of water year (WY), which is related to the volume of runoff occurring. Note that the Critically Dry column in the table was left off as it was only partially visible in the available document.

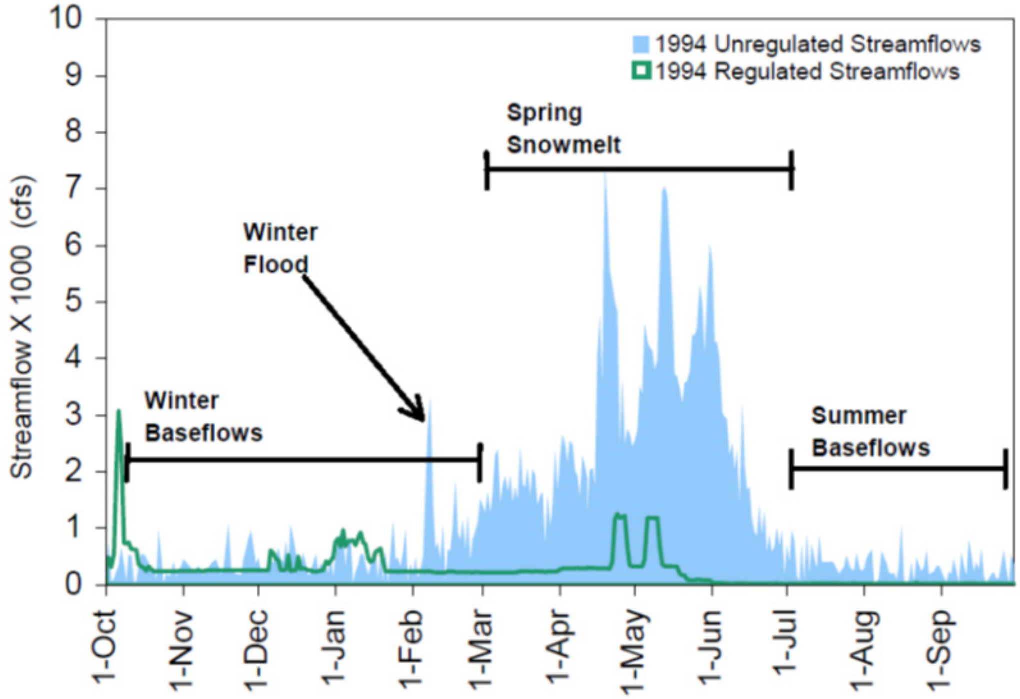
Table 1
Components of Unimpaired Flows for Tuolumne River at La Grange.

Hydrograph Components	Extremely Wet	Wet	Normal	Dry
(probability of exceedence)	20%	40%	60%	80%
(annual water yield, million acre-feet)	>2.55 maf	2.05-2.55 maf	1.39-2.05 maf	1.1-1.39 maf
Fall baseflows (Oct 1-Dec 20)				
Baseflow Average	500	400	400	400
Minimum	230	90	90	130
Maximum	1,700	1,600	900	800
Fall Floods (Oct 1 - Dec 20)				
Median Peak Magnitude	5,300	6,400	2,700	1,800
Maximum	74,400	67,000	15,800	10,600
Median Date of First Fall Storm	4-Nov	18-Nov	30-Oct	18-Nov
Winter Baseflow (Dec 21-Mar 20)				
Baseflow Average	2,800	2,100	1,300	900
Minimum	1,400	1,500	430	570
Maximum	4,500	2,800	2,600	1,700
Winter Floods (Dec 21-Mar 20)				
Average Peak Magnitude	23,700	21,200	14,000	7,300
Median Peak Magnitude	11,800	19,400	10,000	6,100
Minimum	8,500	10,300	5,100	2,900
Maximum	47,600	61,000	38,100	15,600
Snowmelt Floods (Mar 21-Aug 5)				
Average Peak Magnitude	13,400	11,200	8,600	6,800
Median Peak Magnitude	17,500	15,400	12,600	9,600
Minimum	12,200	11,600	10,000	7,400
Maximum	52,100	38,400	43,400	14,400
Snowmelt recession				
Median Date of Peak	1-Jun	16-May	19-May	29-May
Seasonal Duration of Runoff	4-Sep	21-Aug	16-Aug	13-Aug
Summer Baseflow (July 15 - Oct 15)				
Baseflow Average	600	280	220	220
Minimum	400	170	120	130
Maximum	2,300	400	600	400

Source: Reproduced from Table 2-2. "Important components of annual unimpaired hydrographs of daily average flow for the Tuolumne River at La Grange, analyzed for five different water year classes. Based on 1918 to 1997 period." In Habitat Restoration Plan for The Lower Tuolumne River Corridor Final Report, McBain & Trush, 2000.

An illustration of the unimpaired hydrograph for the Tuolumne River at La Grange is shown in Figure 2, along with a comparison to streamflow after implementation of minimum flows in 1996. A Dry WY type is shown.

Figure 2
Annual hydrograph of the Tuolumne River at La Grange comparing unregulated and regulated flow in WY 1994 (Dry WY type).



Source: Habitat Restoration Plan for The Lower Tuolumne River Corridor Final Report McBain & Trush, 2000

2.2.2 Contemporary

Since European settlement there have been numerous alterations to the water, sediment, and wood supply of the Tuolumne River downstream from Don Pedro Dam, as well as to the channel and floodplain. The net result is a reduction in flow, sediment supply, and large wood; limited channel migration; increased channel incision; and an overall degradation of aquatic habitat due to a smaller wetted channel; channel widening, shallowing, and armoring; and reduced lateral bars and riffles (McBain and Trush 2004; Stillwater 2013a).

Placer mining in the mid to late 1800s, dredge mining through the 1960s, and sand and gravel mining from the 1940s through the present have resulted in the removal of gravel and sand from the river channel and floodplain. These activities also left a legacy of tailing deposits between RM 38 and 50.5 and large in-channel pits referred to as special run pools between RM 24 and 52 (Stillwater 2013a). Construction of the La Grange and the Don Pedro dams resulted in the trapping of all coarse sediment supplied by the watershed upstream from the dams. At the same time, farming and grazing has resulted in an increase in fine sediment supply to the river, particularly from several small tributaries between RM 45 and 39. Reductions in peak flows have also reduced sediment transport rates downstream from the dams, but the net effect is a deficit of spawning-sized gravel deposits (estimated loss of 73% of spawning habitat) and an increase in fine sediment deposits compared to historic conditions (McBain and Trush 2004). In response to the deficit of spawning gravel, particularly close to La Grange Dam, gravel augmentation has taken place between 2002 and 2011, adding over 73,000 cubic yards of gravel to riffles close to the dam. Stillwater Sciences (2013b) estimate over 1.3 million square feet of suitable Chinook salmon spawning habitat and close to 350,000 square feet of suitable *O. mykiss* spawning habitat is available at a flow of approximately 225 cfs as of 2012. This spawning habitat is estimated to accommodate a maximum run size of 50,000 to 60,000 Chinook salmon.

In addition to changes within the wetted channel, riparian and floodplain conditions have also been altered by development, bank stabilization, and land use changes. Current riparian conditions show no riparian forest or a very narrow band of riparian vegetation along the active channel (McBain and Trush 2000). Levees, revetments, and limited riparian habitat have resulted in limited rearing habitat being available to juvenile salmonids under current conditions (Stillwater Sciences 2013a).

The average annual water yield below La Grange Dam has been reduced from approximately 1.9 million af to approximately 880,000 af in the period of WY 1996 to WY 2019, a 54% reduction in average annual yield. The lowest annual water yield that occurred between WY 1996 and WY 2019 was 114,000 af in WY 2015; the highest was 3.52 million af in WY 2017. Annual streamflow patterns have changed significantly due to New Don Pedro Dam regulation, including the following:

- loss of inter-annual and seasonal variability
- disruption and complete loss of hydrograph components
- reduction in peak flows
- reduction in baseflows

Minimum streamflows are set for project operations that vary by season and type of WY. Table 2 presents the minimum required streamflows, which were set in 1996 through the Settlement Agreement with the CDFW, U.S. Fish and Wildlife Service, CCSF, and four non-governmental organizations and through a license amendment. The increased flow releases are intended to improve habitat conditions for Chinook salmon.

The Settlement Agreement and license order also provide for the release of pulse flows, the volume of which also varies with WY type. The volume of pulse flows provided by year are shown in Table 2.

Table 2
Minimum Streamflow Schedules for Tuolumne River downstream of La Grange Dam.

Schedule	Units	Critical and Below	Median Critically Dry	Interm. Critically Dry	Median Dry	Interm. Dry-BN	Median Below Normal	Interm. BN-AN[a]	Median Above Normal	Interm. AN-Wet	Median Wet/Max.
Occurrence	%	6.4%	8.0%	6.1%	10.8%	9.1%	10.3%	15.5%	5.1%	15.4%	13.3%
October 1–15	cfs	100	100	150	150	180	200	300	300	300	300
	acre-feet	2,975	2,975	4,463	4,463	5,355	5,950	8,926	8,926	8,926	8,926
Attraction pulse	acre-feet	None	None	None	None	1,676	1,736	5,950	5,950	5,950	5,950
October 16–May 31	cfs	150	150	150	150	180	175	300	300	300	300
	acre-feet	67,835	67,835	67,835	67,835	81,402	79,140	135,669	135,669	135,669	135,669
Out-migration pulse flow	acre-feet	11,091	20,091	32,619	37,060	35,920	60,027	89,882	89,882	89,882	89,882
June 1–September 30	cfs	50	50	50	75	75	75	250	250	250	250
	acre-feet	12,099	12,099	12,099	18,149	18,149	18,149	60,496	60,496	60,496	60,496
Volume (total)	acre-feet	94,000	103,000	117,016	127,507	142,502	165,003	300,923	300,923	300,923	300,923

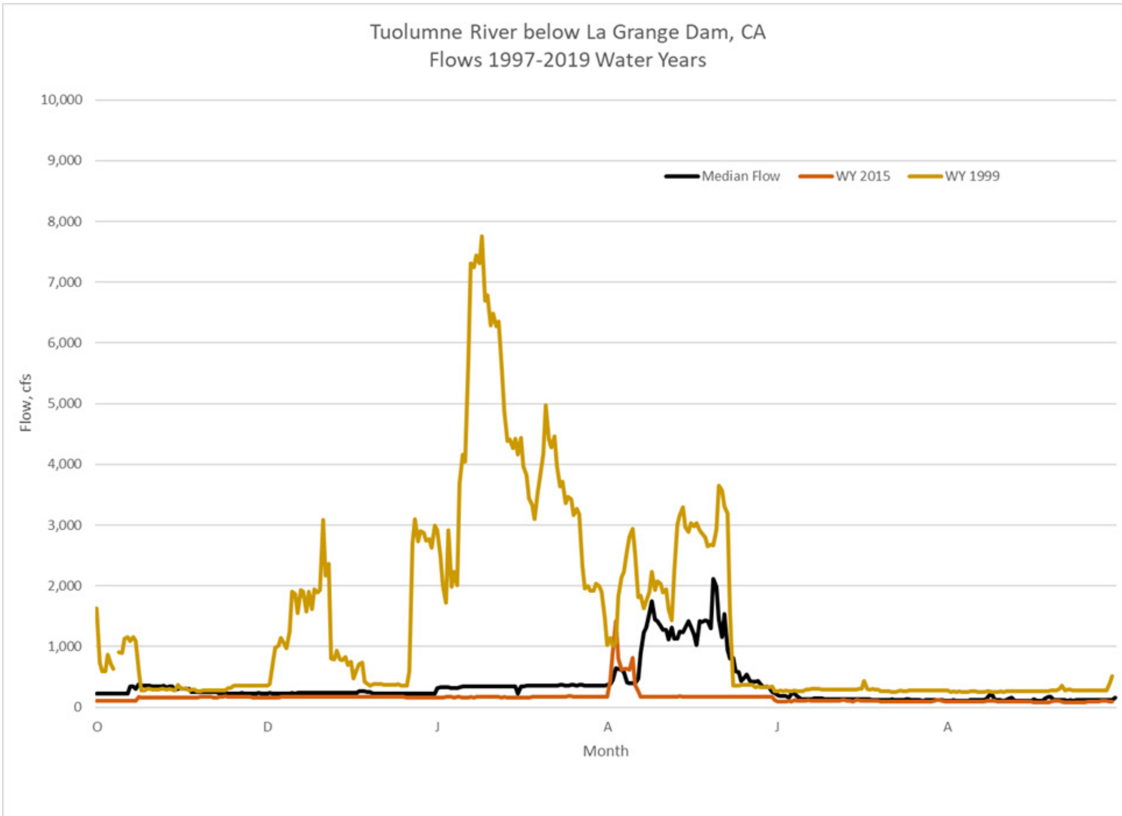
Notes:
Source: Reproduced from Table 2.1.5-1, "Schedule of flow releases to the lower Tuolumne River by water year type contained in the Commission's 1996 order (Source: Districts, 2017a)." In Draft Environmental Impact Statement for Hydropower Licenses, Don Pedro Hydroelectric Project, Project No. 2299-082—California and La Grange Hydroelectric Project, Project No. 14581-002—California, Feb 2019.

a. Between a median critical water year and an intermediate below normal-above normal water year, the precise volume of flow to be released by the Districts each fish flow year is to be determined using accepted methods of interpolation between index values.

AN: above normal
BN: below normal

Flows released from La Grange Dam since adoption of the minimum streamflow schedule are plotted in Figure 3, showing median flows for each day during the period of record analyzed (WY 1997 to 2019) along with Critically Dry (WY 2015) and Wet (WY 1999) years. The figure illustrates that flows in the lower Tuolumne River in all but Wet years lack key components of fall and early winter storm pulses, flow variability, winter floods and the ability to activate floodplain areas except for perhaps short durations, spring snowmelt floods and snowmelt recession, and transition periods between those components.

Figure 3
Tuolumne River streamflow below La Grange Dam.



McBain and Trush (2000) estimated that the mean annual flood (based on annual maximum series) has been reduced from 18,400 cfs to 6,400 cfs; the 1.5-year recurrence event (approximately bankfull discharge) has been reduced from 8,400 cfs to 2,600 cfs. Under the U.S. Army Corps of Engineers 1972 flood control manual, the Districts are required to maintain flood storage space in the New Don Pedro Reservoir and limit instream flows in the Tuolumne River at Modesto (RM 16.2) to 9,000 cfs or less. The resulting effects on flow magnitude and timing have largely altered geomorphic processes, riparian vegetation structure, and recruitment, and have modified aquatic habitats used by Tuolumne River salmonids and other aquatic and riparian species (McBain and Trush 2000).

2.3 Don Pedro and La Grange Dams

The Don Pedro Project (FERC Project No. P-2299) is owned by TID and MID and is located at RM 54.8. The New Don Pedro Dam is 585 feet high and forms the 25-mile long Don Pedro Reservoir that has a capacity of 2,030,000 af (340,000 af are reserved for flood control and 1,381,000 af are available for irrigation, municipal water supply, and hydroelectric generation). A 168-MW powerhouse is located in the base of the main dam. Hereafter we refer to the New Don Pedro Dam as Don Pedro Dam.

La Grange Dam is also owned by TID and MID and is located at RM 52.2 approximately 2.3 miles downstream of Don Pedro Dam. It was constructed in the early 1890s to permit the diversion and delivery of water by gravity to irrigation systems. The dam is 131 feet high and forms a reservoir that extends approximately 1 mile upstream. The dam has no flood control capacity. Irrigation flows into the MID and TID canal works are diverted from the north (right) and south (left) banks of the reservoir, respectively. The La Grange Hydroelectric Project (FERC Project No. P-14581) was completed in 1924. The powerhouse is located approximately 0.2 mile downstream of the dam on the south bank of the Tuolumne River, is supplied with flow from the TID canal, and is owned and operated by TID.

2.4 Chinook Salmon and Oncorhynchus mykiss Population Models

The goal of the Tuolumne River Chinook salmon population model study as described in Stillwater Sciences (2017a) is

> to provide a quantitative salmon production model to investigate the influences of various factors on the life-stage specific production of Chinook salmon in the Tuolumne River, identify critical life stages that may represent a life-history "bottleneck," and compare relative changes in population size between potential alternative management scenarios. Using historical information as well as results of interrelated relicensing studies, the results of this study will be used to assess the extent to which the abundance of juvenile Chinook salmon in the Tuolumne River may be affected by in-river factors.

The goal of the *O. mykiss* population study as described in Stillwater Sciences (2017b) is

> to provide a quantitative population model to investigate the relative influences of various factors on the life-stage specific production of O. mykiss in the Tuolumne River, identify critical life-stages that may represent a life-history "bottleneck," and to compare relative changes in population sizes between potential alternative management scenarios. Using historical information as well as results of interrelated relicensing studies, the results of this study will be used to assess the extent to which the relative abundance of O. mykiss in the Tuolumne River may be affected by in-river factors.

Stillwater Sciences used the term "O. mykiss" to represent both resident and anadromous life history forms in their reports, "rainbow trout" or "resident" to identify resident *O. mykiss*, and "steelhead" or "anadromous" to identify anadromous *O. mykiss*. In this report we used *O. mykiss* to represent both resident and anadromous life history forms and 'steelhead' when specifically referring to the anadromous form.

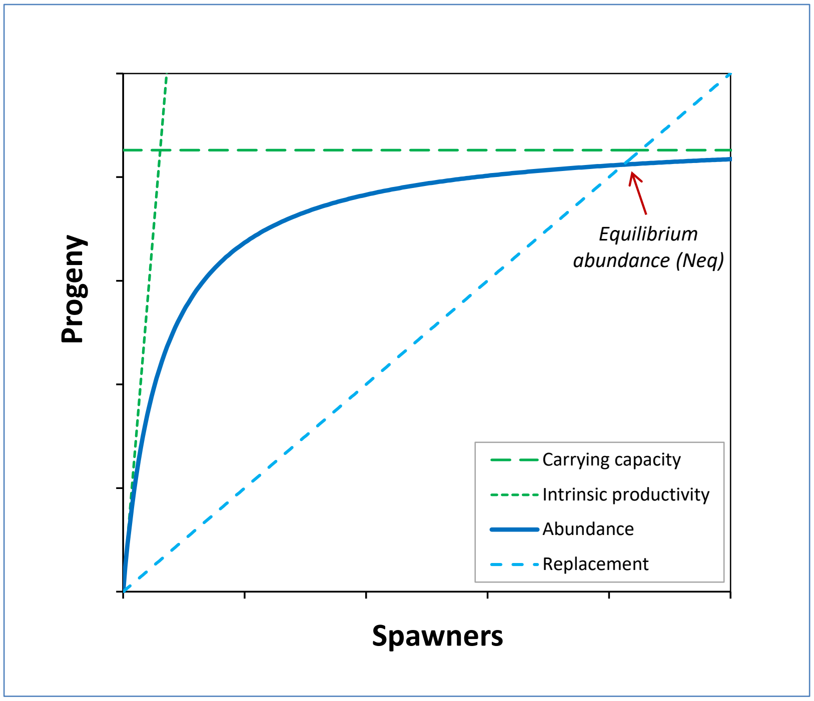
In reviewing the models, we considered how they incorporated foundational aspects of the Viable Salmonid Population (VSP) concept (McElhany et al. 2000). The VSP concept was developed by NOAA Fisheries to define the essential characteristics of a viable salmon population, i.e., one that has less than a 5% probability of extinction over the next 100 years. The concept provides the theoretical basis for assessing different aspects of salmon performance and is used by NOAA Fisheries to assess the long-term viability of salmon populations and in recovery planning for salmon populations listed as threatened or endangered under the ESA. The different facets of the concept also provide a useful approach for evaluating salmon habitat restoration plans, including management of regulated rivers. The components of the VSP concept are often incorporated into salmon habitat and population models, such as the SHIRAZ model (Scheuerell et al. 2006) and the Ecosystem Diagnosis and Treatment Model (Blair et al. 2009).

The VSP concept is defined by four characteristics that describe the performance of a salmon population: abundance, intrinsic productivity,[2] biological diversity, and spatial structure. These four characteristics are often referred to as the VSP parameters. We refer to three of these in our evaluation of the Tuolumne models—all except for spatial structure, which we found to not be useful given the scope of the model and its intended applications.

In addition to the VSP concept, we found it helpful to consider both the inputs and outputs of the Tuolumne population models within a conventional stock-recruitment (S-R) model, also called a spawner-production or spawner-recruitment model or framework. We define here two of the VSP parameters within this framework (abundance and intrinsic productivity; Figure 4). One typical form of the S-R model is called the Beverton-Holt (Beverton and Holt 1957; Hilborn and Walters 1992), which describes the relationship between spawners and their progeny in a manner whereby the number of progeny produced approaches an asymptotic limit or capacity. This form of the S-R model is consistent with how the Tuolumne models were built, as we show later in this report.

[2] McElhany et al. (2000) discuss productivity both as recruits per spawner regardless of spawner level as well as the intrinsic productivity, which is the measure of recruits per spawner at very low spawner density. In this report, we specifically mean intrinsic productivity when we discuss the VSP parameters, which is how it is applied in population dynamics literature (e.g., Hilborn and Walters 1992 and Mobrand et al. 1997).

Figure 4
Stock-recruitment relationship (or spawner-recruitment relationship).



Two parameters determine the shape of the Beverton-Holt production curve in Figure 4. The intrinsic productivity parameter is the slope of the relationship at low spawner density, representing the intrinsic production of the population that would occur in the absence of any competition for resources. This is an extremely important parameter that reflects the capability of the population to withstand stresses such as environmental variability or harvest. Intrinsic productivity is determined by density-independent factors, i.e., those factors that operate without being affected by population density. Capacity is the asymptotic limit for the size of the population as a result of limited resources like food and living space. The effects of habitat capacity on population performance are determined by factors that operate through density-dependence. The difference between the solid blue line and the diagonal replacement line in Figure 4 is called surplus over replacement, and it represents the size of potentially sustainable harvest.

The Beverton-Holt curve indicates where the population would tend to stabilize numerically in the absence of harvest, i.e., where the curve crosses the replacement line. This point, called the equilibrium spawner abundance (Neq), is the result of both the intrinsic productivity and capacity parameters.

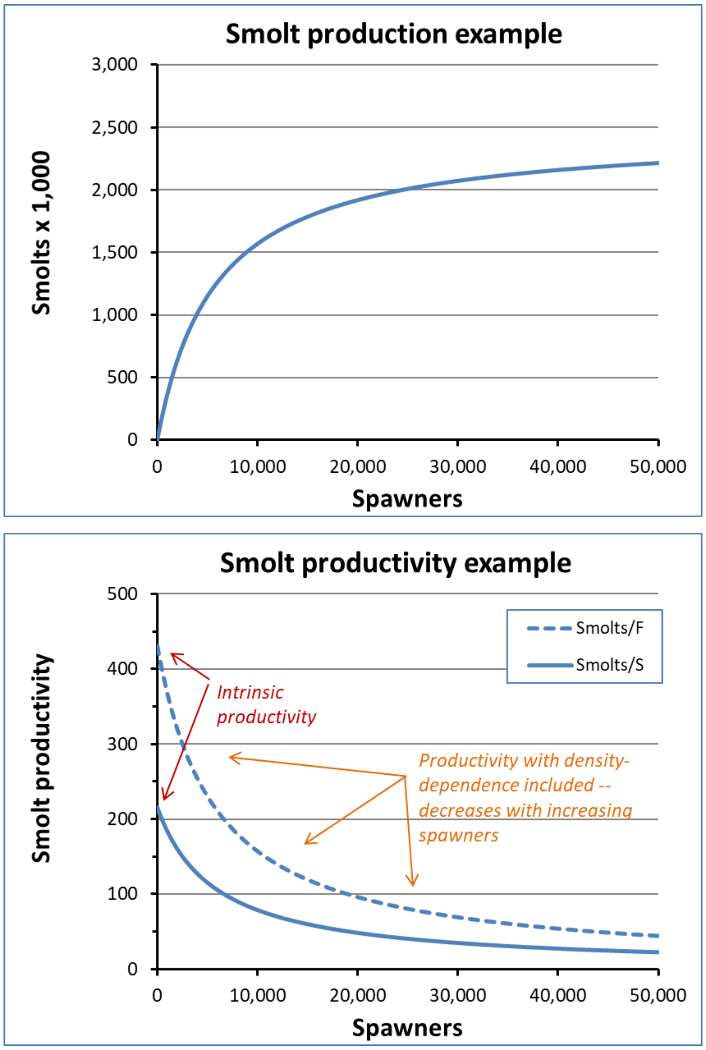
Both of these parameters are determined by the habitat characteristics of the river system (Moussalli and Hilborn 1986; Mobrand et al. 1997; Blair et al. 2009). The intrinsic productivity parameter is determined by habitat quality, i.e., those aspects of habitat that the population does not compete for, such as water temperature and fine sediment within spawning gravels. The capacity parameter is determined by the quantity of habitat in combination with the quality of those habitats. Living space and food, and their quality, are the determinants of capacity.

Figure 5 illustrates the difference between the terms "intrinsic productivity" and "productivity," as the latter is applied in the model reports (Stillwater Sciences 2017a,b). Understanding the difference is essential for following key points in our evaluation of the models, particularly the Chinook salmon model. For the sake of using a realistic example for fall Chinook salmon, we applied data from the Chehalis River in Western Washington, which were derived using modeling to represent current population performance for smolt production (McConnaha et al. 2017).

The top panel in Figure 5 displays expected smolt yield for the fall Chinook salmon population in relation to the number of parent spawners, applying a Beverton-Holt form for the model. The bottom panel in Figure 5 converts the production curve displayed in the top panel to smolts produced per spawner (solid blue line) and smolts produced per female spawner (dashed blue line). The intrinsic productivity value for the smolt population using total spawners is the point where the solid blue line intersects the Y-axis, which in this case is at a value of 215. Similarly, intrinsic productivity can be expressed as smolts produced per female spawner, which is shown as the point where the dashed line intersects the Y-axis and is at a value of 430. We note that in this dataset both numbers exceed 200—the relevance of this point will be made clear later in this report. The bottom panel shows what is meant by "productivity" as it is expressed in the Stillwater Sciences reports. Productivity is seen as a continuum of values, from the highest values (where the lines intersect with the Y-axis that equals intrinsic productivity) to continuously declining values as a function of increasing spawners along the X-axis due to density-dependent factors.

The key point from Figure 5 is that productivity expressed in the Stillwater Science Chinook salmon report is a function of the number of spawners, whereas intrinsic productivity is independent of the number of spawners. However, as described later in this report, the Chinook salmon population model is not a full life-cycle model because it effectively only includes life stages from spawning to smolt emigration, and because the number of spawners is preset so that it is independent of how many smolts are produced. Any consideration of how many spawners might be produced from the preset number of parent spawners is left off—i.e., ignored. Furthermore, how a modeling outcome would affect future generations with regard to population growth rates, or lack thereof, is also ignored. This means that modeling results as presented using smolts per female spawner can only be interpreted in the abstract—what do these values of smolts per female mean for fisheries management and population viability? Within an actual management context, watershed and fisheries management decisions need to ultimately be interpreted as to how actual fish populations are affected.

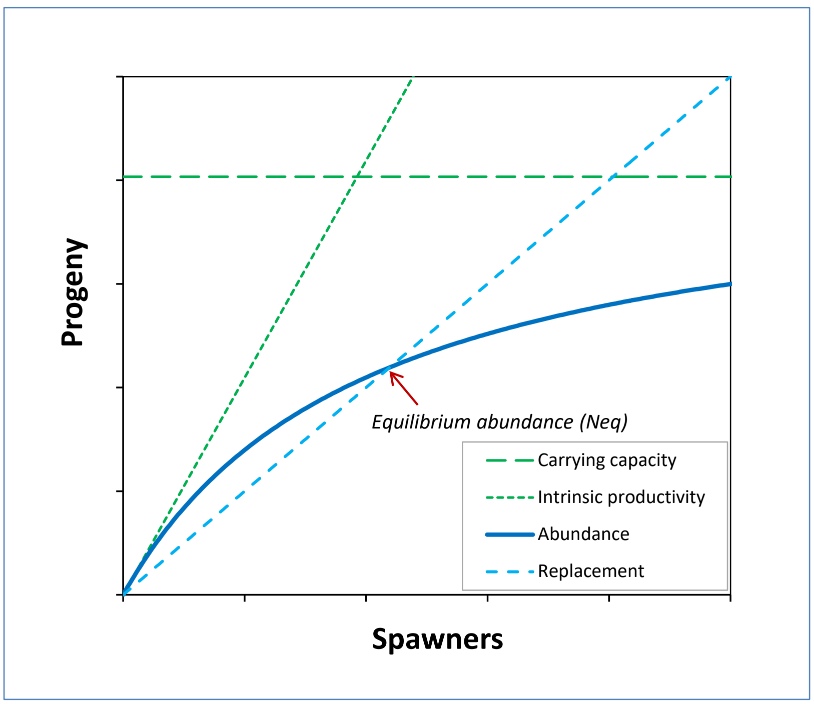
Figure 5
Fall Chinook salmon smolt production and smolt productivity examples from Chehalis River, Washington.



Considering how habitat characteristics affect the capacity and intrinsic productivity parameters begs the question: What is habitat? Most simply, it is the environment from the perspective of a specific species. It is a subset of all environmental conditions that provide for occupancy, survival, and at the appropriate time, reproduction by that species. It is the sum of all of the resources needed by that species, which include food, cover, space, and any special factors needed for survival and reproduction. These factors include chemical properties (e.g., oxygen) and temperature, among others. From the eyes of the focal species, it includes other interacting species, notably predators and competitors. All of these factors comprise the habitat of a given species.

Surplus over replacement also has important meaning for conservation and restoration planning. The greater the surplus over replacement, the more capability the population has to respond to short-term disturbances to the system, such as floods, droughts, heat waves, and downturns in marine survival. The amount of surplus over replacement is affected by both intrinsic productivity and capacity, but intrinsic productivity determines how “flat” the curve is, that is, how close the curve gets to the replacement line on its ascending limb. Figure 6 shows the Beverton-Holt curve with a much-reduced intrinsic productivity value, which flattens the curve. The flatter the curve is to the replacement line, the more likely the population will be adversely affected by floods, climate change trends, and overharvest. In other words, the amount of surplus over replacement, and how flat the curve is relative to the replacement line, is an indicator of resilience in the population to stressors.

Figure 6
Stock-recruitment relationship with reduced intrinsic productivity.



We applied these aspects of population performance, and how habitat affects performance, in evaluating the Tuolumne Chinook salmon and *O. mykiss* models.

3 Physical Models

Three physical models were developed to support the Chinook Salmon Population, the *O. mykiss* Population, and the Floodplain Hydraulic and Habitat models (TID/MID 2019). These include:

- Tuolumne River Operations Model, which includes the Districts' water supply and hydropower operations and the water supply operations of CCSF's Hetch Hetchy system on the Tuolumne River
- Don Pedro Reservoir Temperature Model
- Lower Tuolumne River Temperature Model

These models were developed interdependently and are designed such that the output of one serves as the input for another, including for the Chinook salmon and *O. mykiss* population and habitat models.

3.1 Tuolumne River Operations Model

The Project Operations Water Balance Model Study Report Don Pedro Project FERC No. 2299 (Steiner 2013) describes the development of a model that simulated current operations over a range of historical hydrologic conditions and was used to analyze alternative scenarios for future operations of the Project. The model simulates Project operations for flood control management, water supply, river releases, reservoir levels, and hydropower generation. The study area includes the Tuolumne River from CCSF's O'Shaughnessy, Cherry Valley, and Eleanor dams to USGS Gage 11290000 – Tuolumne River at Modesto.

The objectives of the Operations Model included the following:

- adequate reproduction of observed reservoir levels, reservoir releases, and hydropower
- generation, within acceptable calibration standards over a range of hydrologic conditions
- providing output to inform other studies, analyses, and models
- evaluating alternative scenarios of future Project operations to estimate effects on reservoir levels, reservoir releases, and hydropower generation
- providing the model for use by relicensing participants

The model was prepared using Excel and uses a daily time step for all locations simulated in the model. Figure 7 provides the configuration of the model and location of computation points. For the lower Tuolumne River, flow was computed at the USGS Tuolumne River near La Grange and Tuolumne River at Modesto gages, along with accretion between those points and inflow from Dry Creek.

Figure 7
Operations water balance model measurement and computation points.

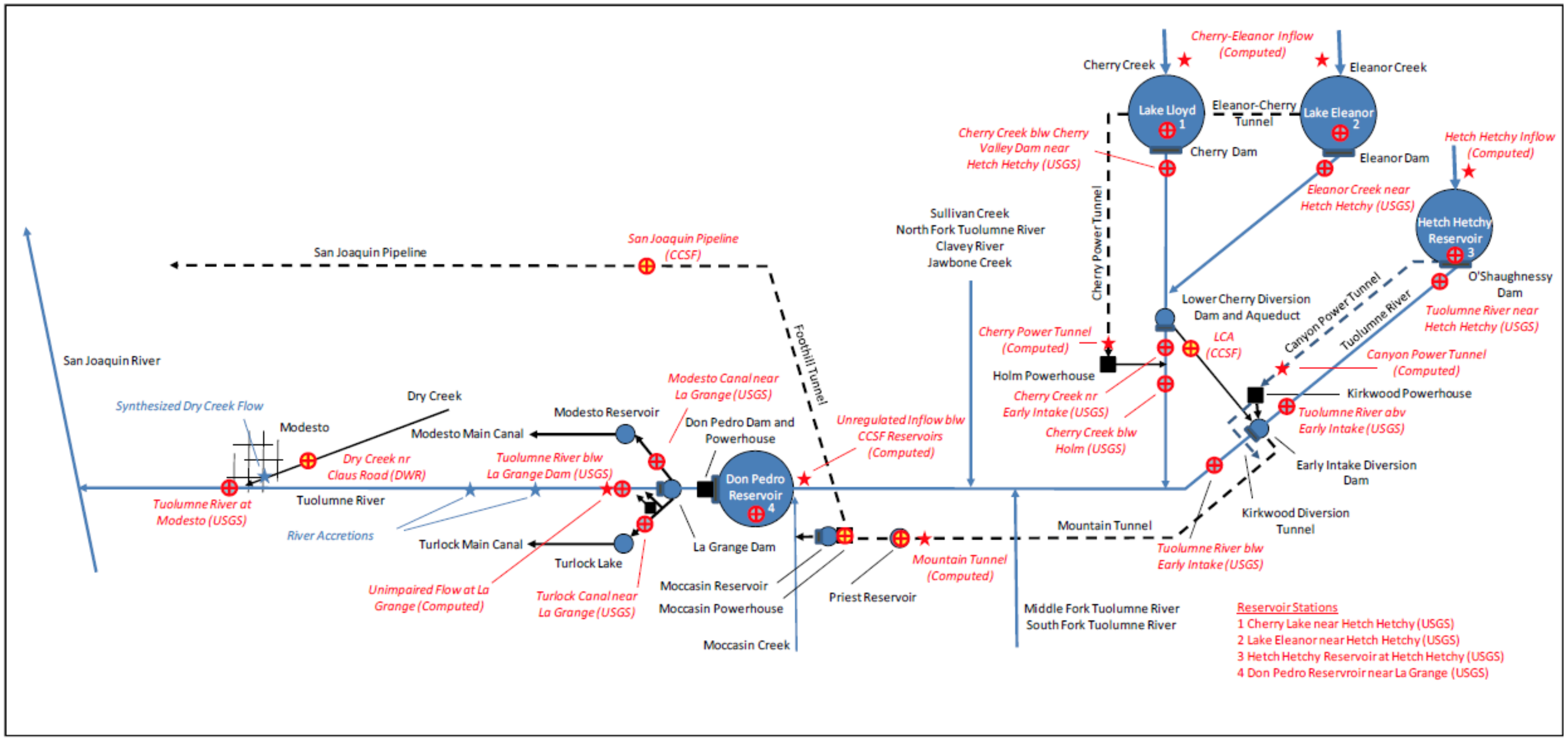


Figure 2.1-1. Tuolumne River Basin hydrologic measurement and computation points.

Source: Study Report W&AR-02 Project Operations/Water Balance Model Attachment A Tuolumne River Daily Operations Model

The simulation period of the Operations Model is WY 1971 through WY 2009. The period of record used for developing and refining the operational rules was the period subsequent to the 1987 to 1992 extended drought period and primarily post-1996. That allows the most recent experience in operations and changes to reflect minimum flow requirements to be represented in the model. We read the modeling reports but did not perform an extensive review of the modeling input, the operating rules in the model, or the output. A comparison of simulated to observed operations of Don Pedro Reservoir was provided and 2 years of output is shown in Figure 8. The comparison indicates the model represents observed operations relatively well. No operations model will exactly match observed as operators make real-time decisions based upon demand for water, observed flows in the river, and other situations. We suggest that an operations model with more capability and flexibility be used in the future, such as the RiverWare model that is commonly used by Reclamation for operational planning in complex river basins.

Figure 8
Simulated and observed storage and release for Don Pedro Reservoir.

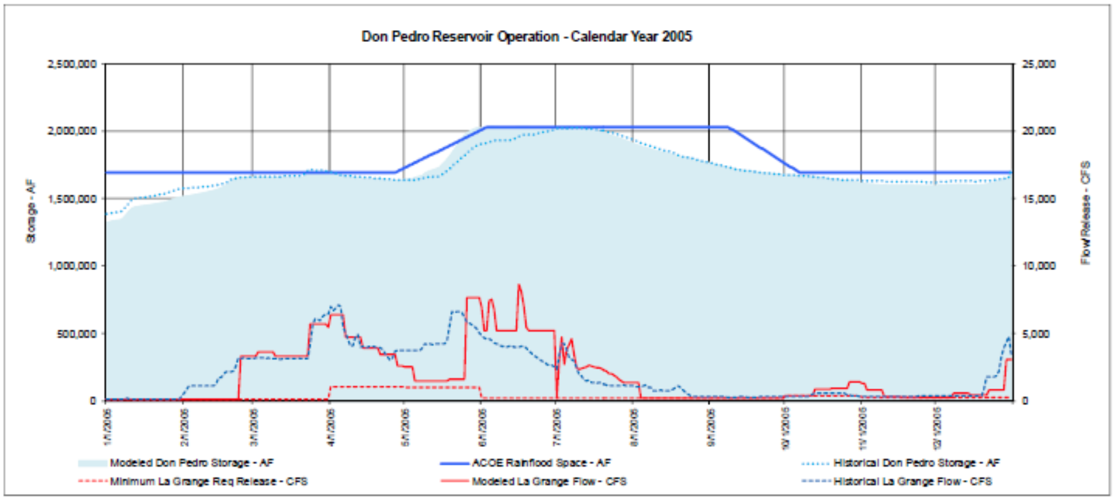


Figure 3.1-6. Historical and modeled Don Pedro Reservoir storage and release - 2005.

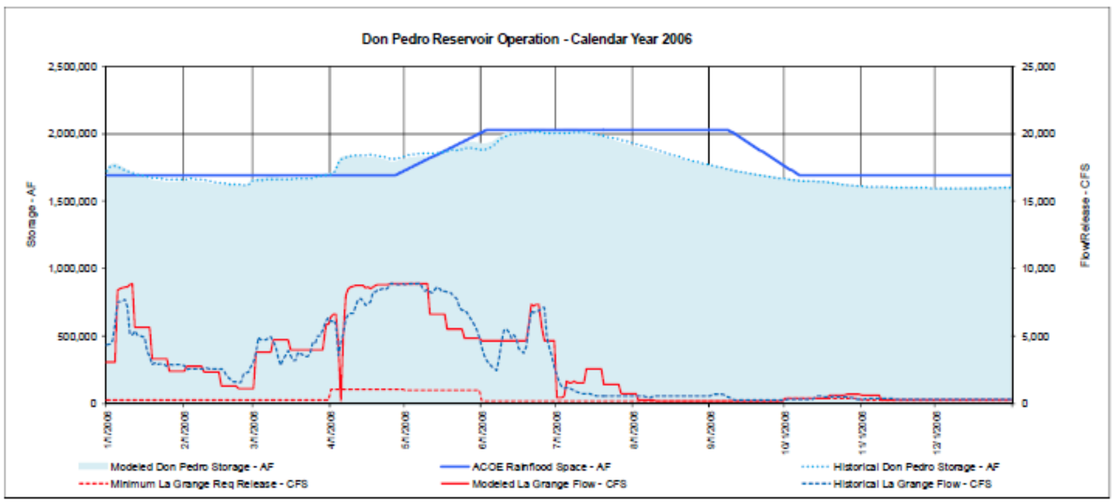


Figure 3.1-7. Historical and modeled Don Pedro Reservoir storage and release - 2006.

Source: Study Report W&AR-02 Project Operations/Water Balance Model Attachment C Model Validation Report

3.2 Don Pedro Reservoir Temperature Model

The Reservoir Temperature Model Study Report Don Pedro Project FERC No. 2299 (HDR 2013) describes the set-up, calibration, and verification of a temperature model for the Don Pedro Reservoir located at RM 54.3.

The objectives of temperature modeling were the following:

- reproduce observed reservoir temperatures, within acceptable calibration standards, over a range of hydrologic conditions
- provide output that can inform other studies, analyses, and models
- predict potential changes in reservoir thermal conditions under alternative future operating scenarios

The hydrology dataset developed for the Tuolumne River Operations Model (W&AR-02) was used as input to the reservoir model. Output from the reservoir model serves as input to the Lower Tuolumne River Temperature Model (Study W&AR-16). The reservoir and river temperature models, working together, also support the Chinook salmon and *O. mykiss* population models developed under studies W&AR-06 and W&AR-10, respectively.

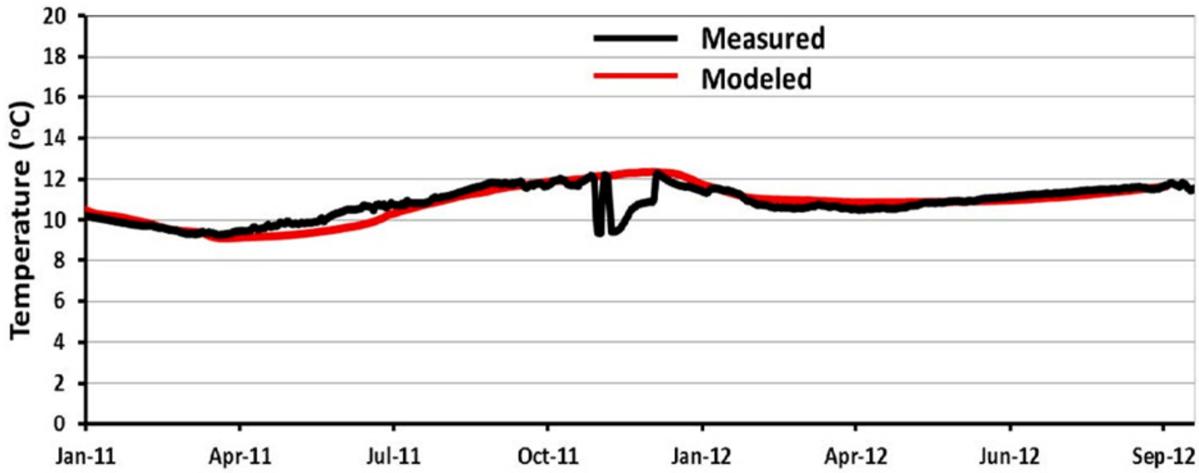
MIKE3-FM, developed by the Danish Hydraulic Institute, was selected for the temperature modeling of the Don Pedro Reservoir. It was selected because a 3D model for the complex reservoir was desired, the model is in extensive use, and it has a graphical user interface that makes the model input and output easier to understand for stakeholders without temperature modeling experience.

The model was prepared using bathymetric and physical structure data along with historical meteorology, hydrology, water temperatures, and operations data. Outflows from Don Pedro Reservoir are routed through the powerhouse intake tunnel at an elevation of 534 feet above mean sea level (MSL). The minimum reservoir level was approximately 598 feet in 1977, and the highest water level reached was approximately 831 feet in 1997. The minimum power pool for Don Pedro Reservoir is 600 feet. The depth of the tunnel allows water at a temperature typically between 10°C and 12°C to be released year-round.

The model was calibrated and verified using data that covers the periods of stratification (April through October) and de-stratification (November through March). Data from 2011 was used for calibration and data from 2012 was used for verification. The report states that the model reproduces the strong vertical stratification of the reservoir and is a good fit to the measured data throughout the year. Our visual review of plots comparing modeled vs measured data supports that conclusion.

For the purposes of fish population modeling in the lower Tuolumne River, the temperature released from Don Pedro Reservoir is the most important aspect of the reservoir temperature modeling study because it is the upstream boundary condition for the Lower Tuolumne River Temperature Model. Figure 9 shows a comparison of the measured and modeled outflow temperatures during the calibration and verification periods. The differences in temperature are not significant compared to the amount of heating that occurs downstream of Don Pedro Reservoir and the model results appear to be adequate for use in the Lower Tuolumne River Temperature Model. The difference between modeled and measured results in November 2011 occurred because of a forced outage by the powerhouse, which resulted in the outlet gates used to release flows. The temperature of that release was 2°C to 3°C cooler than the power tunnel.

Figure 9
Measured and modeled outflow temperatures from Don Pedro Reservoir for 2011–2012.



Source: Don Pedro Relicensing Modeling Tool Updates Meeting, May 18, 2017

3.3 Lower Tuolumne River Temperature Model

The Lower Tuolumne River Temperature Model Amended Study Report Don Pedro Project FERC No. 2299 (HDR 2017) describes the set-up, calibration, and verification of a temperature model between the outlet of the Don Pedro Dam at RM 54.3 and its confluence with the San Joaquin River. The river flows for about a mile after Don Pedro Dam before it enters the impoundment of La Grange Dam at around RM 53.2. La Grange Dam is located at RM 52.2. The model used is HEC-RAS, which is a one-dimensional flow model with temperature modeling capabilities.

The primary objectives of the temperature modeling were to:

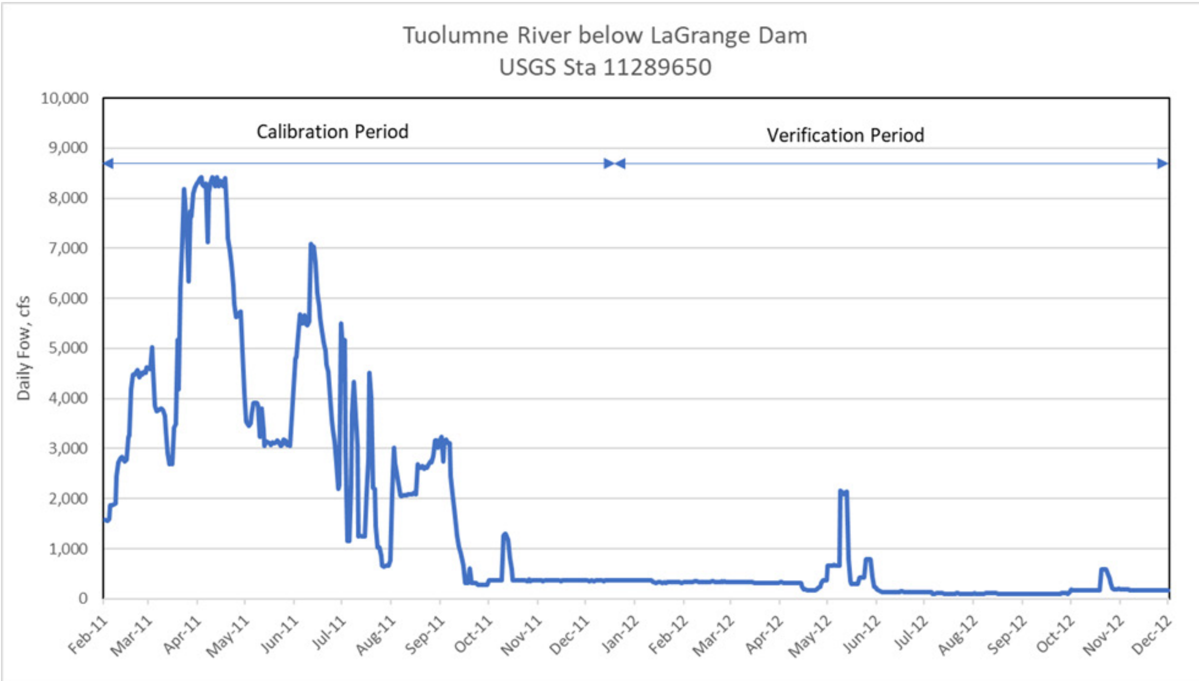
- reproduce observed river water temperatures, within reasonable calibration standards, over the expected range of hydrologic conditions
- determine sensitivity of water temperatures to both flow and meteorological conditions
- provide output to inform other studies, analyses, and models
- predict potential changes in river temperature conditions under alternative future operating conditions

The hydrology dataset developed for the Tuolumne River Operations Model (W&AR-02) was used as input to HEC-RAS. Inflows at the upstream limit of the HEC-RAS model were the computed releases from Don Pedro Reservoir provided by the output of the Operations Model. The river temperature model provides input to the Tuolumne River Chinook Salmon (W&AR-06) and *O. Mykiss* (W&AR-10) population models.

The model was prepared using river cross-sectional data from a number of sources related to the project. The model was calibrated using data from 23 temperature loggers in 2011 and verified using data from the same set of data loggers in 2012. Figure 10 shows the flows at the USGS La Grange gage below La Grange Dam during the calibration and verification period. The year 2011 was a very wet year with an average flow at the La Grange gage of approximately 2,800 cfs. In comparison, 2012 was a relatively dry year with an average flow at the La Grange gage of approximately 270 cfs. The much larger flows in 2011 maintained cooler water temperatures both spatially and temporally than measured in 2012.

Statistical analyses of the differences between modeled and observed temperatures were performed. The mean absolute error (the absolute value of the mean bias) of the daily average flow at the 23 sites in 2011 ranged from 0.1°C below La Grange Dam to 1.0°C at RM 16.2, while in 2012 it ranged from 0.4°C below La Grange Dam to 1.4°C at RM 19. The model is more accurate closer to Don Pedro Reservoir because of the large volume and fairly constant temperature of the releases from the reservoir. The model was not able to represent diurnal fluctuations accurately in some reaches of the river, likely due to unknown groundwater inflows or outflows and the presence of the special run pools, which may act as a thermal buffer because of the large volume of water in the pools.

Figure 10
Tuolumne River flow used in temperature model calibration and verification.



The modeling report concludes that the HEC-RAS model can, with reasonable accuracy, predict water temperatures in the Lower Tuolumne River.

3.4 Physical Models Conclusions

Based on our review, we conclude the temperature model can be used to predict daily average water temperatures with reasonable accuracy (generally within 1.4°C) for different flow regimes proposed for the project. Because the fish population models use daily average temperatures, the predictions are likely satisfactory for use in fish population modeling.

4 Chinook Salmon Population Model

Our review of the Chinook salmon population model is organized into the following sections that address model structure, modeling results, and conclusions.

4.1 Model Structure, Parameterization, Key Assumptions, and Outputs

The Tuolumne River Chinook salmon population model is a spatially explicit (1-dimensional) model that uses an individual-based framework intended to represent the major processes of Chinook salmon spawning, egg incubation, juvenile growth, movement, and mortality to estimate juvenile production as a function of habitat under varying flows and water temperatures in the lower Tuolumne River (Stillwater Sciences 2017a).

It is important to recognize that the model is not a full life-cycle model, as it uses preset, specified numbers of spawners to estimate the number of surviving smolts that emigrate from the river from those spawners. The model makes no attempt to complete the life cycle of the surviving smolts and return them to their natal spawning grounds to begin the next generation. In that sense, the model is limited as it cannot be used to predict equilibrium abundance levels (i.e., average adult abundance over multiple generations) that would be expected to occur under a prescribed set of management actions.

As an individual-based model, it was designed to track each fish within the modeled population along the river on a daily basis, enabling the fish to grow as a function of food availability, water temperature, and population density. The model allows the fish to move in response to density adjustments and flow. Fish advance from the fry stage, to the juvenile (or parr) stage, and finally to a smolt based on their size and whether they are within a prescribed time window consistent with the life history of the species. Individual juvenile fish die as a result of prescribed mortality rates (either a continuous background rate or through an assumed predation rate if the fish is moving or migrating). The model selects a random group of fish to sample for size and status from the large number of fish that need to be tracked, and expands this to the total surviving population to estimate population metrics at given points in space and time.

The model uses a generalized multi-stage stock production approach (Baker 2009) in which starting numbers of a particular life stage (stock) are mathematically modeled to predict how the numbers change as the cohort goes through subsequent life stages. The model incorporates both density-independent and density-dependent survival factors to reflect how habitat quality and quantity along the river is expected to affect population performance by life stage. The model, therefore, incorporates the conventional population dynamics concepts of both intrinsic productivity and habitat capacity used in assessing salmon population performance (Hilborn and Walters 1992; McElhany et al. 2000) and as described above in Section 2.4.

The model incorporates river flow and water temperature data for prescribed locations along the entire river on a daily basis for a given WY. A dataset with 42 WYs representing the period of record from 1972 to 2012 that contains daily flow values and water temperatures is packaged with the model for analysis.

Model parameters that determine the expected effect on the survival factors affecting individual fish are defined by discrete numbers or ranges depending on certain attributes of the individual fish being tracked in the model, such as fish size and life stage.

The model also includes random elements for many mechanisms affecting life history progression, relying on probability distributions for events such as adult upstream migration timing (i.e., the timing of the spawning run, which is a model input), individual spawner age, spawning locations, fry and juvenile movements, predation related mortality, as well as size of fish at the point of fry and smolt emigration. Spawning fish are distributed in a manner to use the available spawning habitat. Spawning location is based on a pre-set distribution of spawning location preferences based on redd mapping conducted in 2012 (TID/MID 2013b). We note that once an individual spawner arrives at a given spawning location, in the model it stays there and does not redistribute in relation to overall spawning density (page 4-23, Stillwater Sciences 2017a).

At low spawning densities the spawners exhibit little spatial overlap in where redds are built, though some degree of redd superimposition still occurs. The amount of redd superimposition increases at higher spawning densities, which in the model acts to reduce the survival of the total eggs deposited. Hence the effect of density-dependent mortality on egg survival increases as the number of spawners increases.

Each stock production component in the model also makes use of temporally and spatially varying environmental conditions while determining the progression of individuals within their respective life stages and promotion into the next life stage.

Of particular importance to modeling outcomes is how the model handles the movement of fry, juveniles (parr), and smolts beginning with emergence from the gravel and continuing until they either die or exit the river. These movements are treated as four separate groups of fish: 1) post-emergent fry that exit the river very quickly, a group sometimes referred to as fry migrants in the Chinook salmon literature (Healey 1991); 2) fry emigrants that experience some rearing and growth in the river prior to exiting the river; 3) juvenile emigrants that rear in the river for a considerable period, gradually moving down the river, until survivors exit the river prior to attaining smolt status; and 4) smolts, that is, those fish that have reared in the river long enough to grow to a size to be considered a true smolt, which then relatively rapidly exit the river. The model also assumes that a fixed percentage of the fish that attain smolt size (10%) do not leave the river as smolts but residualize in the river and continue to rear, and presumably if they survive overwinter, could smolt and leave the river as yearling smolts.

Movement of fish being tracked in the model is an important determinant of the results that are projected by the model. A fixed percentage of 30% of all newly emerged fry (or swim-up fry) are assumed to emigrate directly and immediately out of the river following their emergence from incubation sites. In the model, these fish have no contribution to what are considered viable offspring that survive to the smolt stage and, therefore, are not incorporated into the metric for estimated smolts per female spawner.

Following the initial and immediate movement of newly emerged fry out of the river, in the model the remaining 70% of fry begin to rear, gradually moving downstream, growing as they go or dying according to preset rules within the model. Predation mortality applied in the model is only assumed to occur on moving fry (and subsequently on moving parr-sized fish and smolts). Fry movement is triggered when habitat capacity is exceeded. Fry-sized fish (<50 millimeters [mm]) that move enough to reach the mouth of the river are allowed to exit the river. These fish are called fry emigrants in the model. As with the newly emerged fry that leave the river immediately, fry emigrants leave the river as fry and make no contribution to the metric smolts per female spawner—therefore, in effect they are treated as mortality.

Fry that grow to a size of 50 mm while still in the river are promoted in the model to the juvenile (or parr) life stage, where they continue to rear, grow, and move by essentially the same rules applied to fry-sized fish as described above.

Mortality within the model on both fry and juveniles while in the Tuolumne River appears to operate mainly through density-independence, though the amount of mortality varies as to whether habitat capacity is exceeded or not; therefore, there is an interaction with habitat capacity in this regard. Juveniles can also succumb to high temperatures if certain temperature thresholds are exceeded.

Similar to fry emigrants, juveniles can reach the mouth of the river prior to dying. If they do, these fish are moved out of the river and do not contribute to the smolt population. Page 4-27 in Stillwater Sciences (2017a) states "juveniles which die or leave the Tuolumne River before attaining smolt status are labeled as dead juvenile and are passed into the dead juvenile life stage." We note, however, that in the Stillwater Sciences Technical Memorandum dated July 3, 2020 (Appendix A), the authors stated "As with fry, rearing parr-sized fish that pass the downstream Grayson (RM 3.5) RST and out of the Tuolumne River are not counted as mortalities but do not contribute to later smolt emigration totals and estimates of smolt productivity (smolts per female spawner) from the Tuolumne River." Whether these fish are counted as mortalities or not is therefore unclear—the important point of this discrepancy between the report and the Technical Memorandum in terms of modeling output is that these fish do not contribute to smolt productivity.

The documentation in the report as to whether these moving juveniles can make it to the mouth of the river in the model is also confusing. Page 4-15 (Stillwater Sciences 2017a) states that juveniles are assumed to not emigrate from the river. However, page 4-27 states that those juveniles that make it to the mouth of the river and leave the river before attaining smolt status are labeled as dead juveniles. Stillwater Sciences clarified that juvenile emigration is represented in the same way as for rearing fry but using different parameter values to match seasonal seining distributions and RST passage estimates (see response to question 3 in Appendix A).

Once a fish attains smolt size (note that some variability on size appears to be used in the model) it attains smolt status. At the point that this status for a fish is achieved, the model reports these fish as "smolts produced." The total of all of these fish represents the total number of smolts produced by the river. This is an important metric that is output by the model; however, this number of fish is not reported in the modeling report (Stillwater Sciences 2017a) nor is it the number used to compute the number of smolts per female given in the modeling report or TID/MID (2019).

Once fish attain smolt status (smolts produced), they begin their smolt migration from the river. As with moving fry and juveniles, smolts that are moving are subjected to a mortality rate assumed to be due to predation. Smolts that survive their migration within the Tuolumne River are called "smolt emigrants" in the model, which are the smolts assumed to exit the river. The number of smolt emigrants is used to compute the metric termed "smolts per female spawner," which is the key metric discussed in Stillwater Sciences (2017a) and TID/MID (2019).

Predation is assumed to be the greatest cause of mortality in the model. Predation mortality rates are applied to moving fry (i.e., to the 70% of fry that do not emigrate immediately upon emergence), moving juveniles, and to smolts, which by their nature are also moving. These predation mortality rates are based entirely on the analysis of RST data from Robichaud and English (2017), which were derived for fish considered to be smolts and were applied to fry and juveniles. However, the actual mortality rates used in the model for these three life stages differ and Stillwater Sciences (2017a) does not explain how the estimates of mortality derived for smolts were used to derive the mortality rates applied to fry and juveniles in the model.

The modeling report summarizes all results in terms of smolt emigrants per female spawner. This metric is referred to as productivity. As discussed earlier, this metric is not equivalent to intrinsic productivity, which does not consider any effect of population density (see Section 2.4). Therefore, the reader needs to recognize that the number of female spawners being applied in a given model run can have a substantial effect on the metric of smolt emigrants per female through density-dependent mechanisms.

The actual modeling output, which is not reported in Stillwater Sciences (2017a), includes the following parameters for each WY being modeled:

- Number of newly emerged fry (the model refers to these fish as "swimups")
- Number of emigrant fry
- Number of smolts produced (at the outset of smolt migration)
- Number of emigrant smolts (those that survive to the mouth of the river)
- Metrics on timing of smolts and smolt sizes

The model also reports the number of surviving juveniles that do not smolt and are assumed to continue to rear in the river after the smolt migration ends. Ten percent of all fish that would be eligible to be promoted to smolt status are assumed to residualize and continue to rear in the river. The model does not follow the fate of these fish and these fish are assumed to not contribute to smolt production from the river. We note that the total number of residual juveniles that could continue to rear in the model can be very large, depending on the number of spawners being modeled (see Figure 15).

4.1.1 RST-Based Survival Estimates and Flow-to-Survival Relationship

Estimates for Chinook salmon are based on many factors in the model that come together in the form of estimates of smolts collected at the Waterford (RM 29.8) and Grayson (RM 5.2) RSTs and the relative smolt passage success between the upper and lower RSTs using the relationship in Equation 8 (Stillwater Sciences 2017a). To represent predation mortality of outmigrant smolts from the entire river, survival between the RSTs as a function of flow is converted to survival per unit distance travelled per Equation 9 (Stillwater Sciences 2017a) and applied to the rest of the lower Tuolumne River. In addition, these estimates were applied to fry emigrants and juvenile emigrants once they began moving downstream in the Chinook salmon population model. The *O. mykiss* population model uses the survival relationships developed for Chinook salmon smolts. Thus, the RST smolt catch data and survival estimates between the RSTs based on these data were applied to all Chinook salmon life stages and to all *O. mykiss* juveniles when these fish were moving downstream.

Because the RST catch data and survival estimates are foundational to the results from both models, they were a focal element of our review. We provide the following six observations:

1. In general, RSTs are good for documenting presence, absence, timing, and behavior related to environmental conditions, but developing production estimates based on RST catch and efficiency trials is challenging.

This is well documented in the scientific literature. Volkhardt et al. (2007) state that discharge is one of the primary factors associated with fish migration and can strongly affect trapping efficiency. Pilger et al. (2019) point out that abundance estimates from RST data depend on estimating a trap's efficiency via mark-recapture releases, these estimates can be highly uncertain because they are variable and influenced by many factors, and it is important to estimate uncertainty associated with any abundance estimate. They conclude that understanding the sources of uncertainty is necessary to ensure that estimates used in life cycle and S-R modeling are of high quality.

To address one aspect of mark-recapture modeling, overdispersion (i.e., the schooling behavior common to outmigrating juvenile salmonids), Mäntyniemi and Romakkaniemi (2002) developed a Bayesian probability model for mark-recapture data and found that model structure assumptions can have a substantial impact on estimated size of a smolt run, especially in terms of the precision of the estimate.

Pilger et al. (2019) compared estimated abundances in the Stanislaus River RSTs using a long-term dataset (1996 to 2017) across five methods that differed in their treatment of trap efficiency (stratified versus modeled) and statistical approach. Their goal was to assess the variability of estimates across methods and to evaluate whether the method used affected trends in estimated abundance. The results of this study are encouraging. They reported that estimated abundances in the Stanislaus River using the procedures evaluated were generally robust regardless of the method used, and estimated juvenile abundances were significantly related to adult escapement counts.

While many mark-recapture RST efficiency trials have been completed in the Tuolumne River, the analysis of the data beyond developing annual estimates of catch appears limited to Robichaud and English (2017) and a similar analysis conducted in 2012. Given the influence that survival estimates and the flow-to-survival relationship have in estimating production in both population models, and given the long-term data base available in the Tuolumne River, additional analysis of Tuolumne River data similar to Pilger et al. (2019) is warranted.

One difference between the Stanislaus River and the Tuolumne River is that data are collected at one RST in the Stanislaus River (Oakdale, RM 39.9), whereas two traps are operated in the Tuolumne River. If the Tuolumne River had only one RST and that was the Waterford trap, one would conclude as Stillwater Sciences (2017a) did that model predictions did not match smolt passage well at this location, and modelers would likely attempt to adjust the model to better fit the empirical data. Because the model attempts to predict numbers of fish as they recruit from one life stage to the next, and it tracks the fish as they move from one segment of the river to another, it is clear based on the performance of the model at predicting numbers of smolts at the Waterford site (Table 5.1-1, Stillwater Sciences 2017a), that the model is not correctly predicting recruitment from one life stage to the next or trajectories of fish abundance throughout the river. This brings into question whether the model can predict limiting habitat factors or life stages and actions to address them. This question is especially relevant knowing that most if not all spawning occurs upstream from the Waterford RST. In contrast, if the only trap on the Tuolumne River was the Grayson RST, one would likely conclude (as was apparently the case based on Stillwater Sciences 2017a) the model predictions more closely fit the empirical data and make fewer adjustments to the model. Also, it appears to us that if one modified the model to more closely match empirical data collected at the Waterford RST, model estimates at the Grayson site may not match empirical data collected at the Grayson RST.

We did not find an explanation for why Robichaud and English (2017) excluded 7 data periods in 2007, 2009, 2010, and 2011 from their analysis that represented ascending flow conditions (Figure 1; Robichaud and English 2017). It is well established that such periods stimulate juvenile salmon movement, and this can be seen in the sharp increases in smolt counts at both Waterford and Grayson RSTs (Figures 3, 5, and 6 in Robichaud and English 2017). The influence and sensitivity of RST catch with ascending flow periods included in the analysis should be assessed.

Our calculations of smolt survival between the RSTs based on estimates of smolt passage presented in Table B-3 (Stillwater Sciences 2013a) for years with common sampling (2006, 2008, 2009, 2010, and 2011) indicated that survival varied greatly and ranged from 14% in 2010 (Above Normal WY) to 255% in 2011 (Wet WY). This suggests that multiple factors (e.g., flow, capture efficiency, life stage, true survival between the RSTs, rearing, and behavior) are interacting. For example, was high RST catch of fry in 2011 due to favorable environmental conditions that supported production, even though total escapement in 2010 was estimated at only 540 Chinook salmon (GrandTab database maintained by CDFW dated 2019.05.07), or due to improved catchability caused by increased velocity at the RST intakes, or a combination of factors? Was the apparent transition of fry to smolts between the traps responsible for the 255% increase in estimated smolts at the Grayson RST? This is difficult to imagine given a presumed high speed of travel of fry between the RSTs under high-flow conditions that year. Alternatively, were smolts passing the Waterford RST undetected due to conditions that year that were then detected at the Grayson RST? These interacting factors need to be addressed in an analytical framework to understand their influence on estimated survival.

The comments above suggest that additional analyses of Tuolumne River data are needed to investigate factors associated with trap efficiency, variability across years, and mark-recapture releases to develop best-fit models for each trap and life stage that address all WY types and data dispersion (data appear to be overdispersed). The analyses should include approaches similar to Pilger et al. (2019). Estimated survival to each trap and between the RTSs could also be independently verified using telemetry methodologies (see Section 6.3). This could help inform whether having to estimate catch at two traps influences estimated survival, where effects of multiple factors on trapping efficiency are incorporated into catch at two traps, compared to a single trap in most rivers where catch at the single trap is expanded to estimate abundance.

2. Flow-to-survival relationship lacks confidence intervals.

Uncertainty associated with the survival-to-flow relationship needs to be characterized and could be estimated based on the relationships developed in Figure 10 of Robichaud and English (2017).

Table 3 of Robichaud and English (2017) provides confidence intervals around each mark-recapture trial, which were small. For example, interval 11c at Waterford in 2011 shows an estimated survival of 49.4% with a 95% confidence interval from 48.9% to 50.0%. However, the variability among trials is not presented in the relationships between flow and survival. For example, survival in Figure 10 (Robichaud and English 2017) around 3,000 cfs ranges from 0% to approximately 50%. The lack of confidence intervals (more appropriately, prediction intervals) around the linear regression selected for Chinook salmon modeling projects a false sense of precision in estimated smolts produced per female spawner. Presenting confidence intervals with the regression and carrying the variability forward into estimated smolts produced per female is essential for interpreting differences among the alternatives being evaluated. Pilger et al. (2019) acknowledged this risk by stating "Evaluating abundance trends based on a single estimation approach without knowing its level of uncertainty is difficult at best, and at worst can provide misleading results about a species' critical life stage."

3. The linear regression selected to estimate smolt abundance as a function of flow has a low R^2.

Robichaud and English (2017) reanalyzed survival between the RSTs as a function of discharge measured at USGS Gage 11289650 at La Grange and plotted linear regressions on the raw and arcsine-transformed data along with results of a univariate general linear model (GLM). In all cases, R^2 values were low and ranged from 0.14 to 0.18. In contrast, Mesick and Marsten (Figure 15; 2007) reported a R^2 of 0.82 for the relationship between the number of smolt-sized Chinook salmon outmigrants (FL > 70 mm) passing the Grayson RST and flow at La Grange between March 1 and June 15 from 1998 to 2006. The cause of these differences in the proportion of the variance in survival that is explained by flow among the modeled relationships is not clear and warrants further investigation.

4. Additional flow-to-survival relationships are available.

According to Table 4.2-5 and Equation 8 (Stillwater Sciences 2017a), the relationship between survival and flow selected for estimating survival between the RSTs results in an increase in survival of 0.00002347 per cfs. It is not clear why a linear flow-survival relationship fitted to RST data was selected for modeling smolt outmigration survival. The reason presented in the report is that this was done to provide consistency with RST data used in model fitting, but that reasoning is not instructive. In addition, the fitted intercept of survival in Equation 8 at zero flow is 0.03287, which makes no sense biologically. With zero flow survival would be zero. The regression should be forced through the intercept and the relationship estimated, which will steepen the slope of the relationship somewhat. Based on a visual interpretation of Figure 10 in Robichaud and English (2017), this would also change the shape of the relationship to one that is curvilinear and that increases sharply as flow increases from zero and then flattens out at higher flows.

Robichaud and English (2017) reanalyzed the available survival data and developed several flow-to-survival relationships. They reported that the linear relationship between survival and mean flow was significant ($P = 0.002$) as was the slope of the arcsine-transformed model ($P < 0.001$), although the R^2 for each relationship was low at 0.18 and 0.15, respectively. Their univariate GLM indicated that flow was a statistically significant factor in predicting survival ($P = 0.006$). However, the R^2 of the univariate model was still low (0.14), and the effect of the exclusion of the single highest survival point (49.4% in 2011) produced shallower slopes (i.e., lower predicted survival values) with small effects on improving R^2. Because survival data were overdispersed, the GLMs were recalculated using a 'quasibinomial' fit. The multivariate quasibinomial GLM showed that abundance was the most important factor ($P < 0.0001$) in predicting survival, while turbidity, flow and temperature did not improve the model. The approximate R^2 of the multivariate model was 0.41.

The multivariate quasibinomial GLM had the highest R^2, meaning the observed variation in survival is best explained by the model's inputs using this relationship, but this model was not selected for reasons that were not explained. Clearly the issue of overdispersion was recognized and addressed. At a minimum, sensitivity runs using the multivariate quasibinomial GLM-based relationship between smolt survival and flow should be conducted to understand how Chinook salmon model outputs vary with the relationship selected for the population model. Also, model fit was highly sensitive to the one data point from 2011 with very high abundance and survival. We found no explanation as to why 2011 was removed or why model runs with and without 2011 were not conducted to inform the sensitivity of model outputs to this data point. Robichaud and English (2017) acknowledges this by stating "There continued to be a positive and significant relationship between survival from Waterford to Grayson and river flow, although the exact relationships were sensitive to outlier values."

The influence of including 2011 data on which flow-to-survival relationship is selected for use in the Chinook salmon population model is large. Based on Equation 8 (Stillwater Sciences 2017a), increasing flow an order of magnitude from 300 to 3,000 cfs results in survival increasing from 4% to 10%. While that is a large relative increase, survival of 10% based on the linear regression is much different than the approximately 40% survival at 3,000 cfs indicated by Figure 11 (Robichaud and English 2017) based on the multivariate quasibinomial GLM when year 2011 is included in the analysis.

As described in Section 4.2.1, we examined the effect of increasing the slope parameter of the smolt-to-smolt survival relationship used in the model by increasing the slope to approximately match the higher regression line seen in Figure 9 of Appendix C in Stillwater Sciences (2017a) (see Figure 16).

There are several lines of evidence that the flow-to-survival relationship may be more robust than indicated by Equation 8, and that supports our recommendation for further data analysis (see Section 6.3). In the Tuolumne River, Table 5-3 in Stillwater Sciences (2013a) provides evidence that the estimated number of outmigrating Chinook salmon fry, parr, and smolts is substantially greater in years with high spring flows (e.g., Wet WY types occurring in 1998, 2005, 2006, and 2011). Also, Figure B-10 in Stillwater Sciences (2013a) provides evidence that the flow-to-smolt survival relationship in the Tuolumne River is strong enough to be observed as far downstream as the Mossdale Kodiak trawl in the lower San Joaquin River, even given flow attribution. The report interprets this as support for the hypothesis that flow reduces predation related mortality in the lower Tuolumne River. In addition, Mesick et al. (2008) identify a substantial and positive relationship between the number of smolt-sized Chinook salmon outmigrants passing the Grayson RST plotted with flows at La Grange, with an adjusted R^2 of 0.73 according to the figure caption and 0.82 according to the text.

We also note there is evidence that flow benefits may extend downstream from the Tuolumne River. Mesick and Marsten (2007) summarized earlier trend analysis suggesting that the number of natural- and hatchery-origin adult Chinook salmon that returned to the lower Tuolumne River was strongly correlated with flow during juvenile migrations in spring (e.g., April and May). The effects of flow on adult recruitment may result from changes in habitat conditions within or downstream of the Tuolumne River. Buchanan and Skalski (2020) reported that survival of acoustically tagged, hatchery-origin fall Chinook salmon in the upstream (riverine) region of the Delta was positively associated with San Joaquin River flow and average net flow in the interior Delta. However, they also noted the effect did not appear to carry through the Delta, as higher survival to Delta exit was associated with higher root mean square of flow in the tidally influenced interior Delta but not with higher San Joaquin River flow, which suggested to the authors that different mechanisms were influencing survival in the upstream versus downstream reaches of the Delta.

Flow benefitting survival is broadly reported in the literature, including other basins in California. For example, Zeug et al. (2014) analyzed 14 years of RST data and found a strong, positive response in survival, the proportion of pre-smolt migrants, and the size of smolts when cumulative flow and flow variance were greater. They concluded that periods of high discharge when combined with variance in high discharge are important for migrant size, successful emigration, and the maintenance of diverse migration strategies. The positive relationship between flow and smolt survival has been observed through adult recruitment. In the Sacramento River, Michel (2018) evaluated 20 years of data on three Chinook salmon populations and found that streamflow during outmigration had a higher correlation with smolt-to-adult recruit survival (SAR) than two marine productivity indices. He concluded that although abnormally poor marine conditions reduce SAR, most interannual fluctuations in SAR were explained by outmigration survival during the freshwater life stage.

5. Model calibration or validation was poor in some cases.

Estimated Chinook salmon smolt passage produced by the Chinook salmon model at the Waterford RST and fry passage at the Grayson RST did not match the estimated abundances based on RST catch (Table 5.1-1, Stillwater Sciences 2017a), but was accepted based primarily on passage timing (Section 5.1, Stillwater Sciences 2017a). The mismatch between model estimates and RST-based estimates of smolts at Waterford is apparent in Figures 5.1-1 and 5.1-2 (Stillwater Sciences 2017a). The influence of the mismatch on model results is not discussed, presumably because model fit to Grayson smolts, the metric used to assess management alternatives, appears to be better (Table 5.1-1, Stillwater Sciences 2017a). However, because survival between the RSTs is a foundational element of the model framework, the mismatch between model estimates and estimated smolt passage at Waterford warrants further explanation.

Updates to the Chinook salmon model validation in the 2013 study report was conducted to assess the degree to which predictions from the recalibrated model agreed with available field-based data. Based on the top panel of Figure 2.4-1 in Attachment A (Stillwater Sciences 2017a), the Chinook salmon population model overestimated smolt passage at Waterford compared to observed passage in 5 of the 10 comparisons shown, especially in 2012 and 2013. In the remaining comparisons the estimates at Waterford were generally similar to the RST passage estimates except for 2006, when it was substantially less than the RST estimate. We did not find any explanations or discussion of the importance of the differences between modeled and observed passage estimate of smolts at the Waterford RST. Because the model estimates numbers of fish as they recruit from one life stage to the next and tracks fish as they move from one segment of the river to another, and passage estimates at Waterford and Grayson are used to estimate survival between the RSTs that are then expanded to the entire river for all Chinook salmon life stages and for both species, understanding why there are differences between modeled and observed passage estimates of smolts at the Waterford RST is critical to accepting model outputs. Additional analysis of how differences between modeled and observed passage estimates at Waterford influence model outputs is warranted.

Based on Figure 2.4-3 in Attachment A (Stillwater Sciences 2017a), the model appears to be over estimating productivity in the low range (<10 smolts/spawner) and underestimating it in the high range (>10 smolt/spawner).

6. Different juvenile abundance values reported.

In reviewing the available information, we noted differences in values presented and the lack of an explanation for this hindered model interpretation. For example, in Table B-3, Stillwater Sciences (2013a), the estimated number of fry passing the Waterford RST in 2011 is reported as 400,478 fish, whereas Table 5.1-1 (Stillwater Sciences 2017a) reports that 284,444 fry passed the Waterford RST in 2011. Values for smolts that year and location are reported as 15,608 and 74,494 in the two reports, respectively.

4.1.2 Model Structure Conclusions

Model structure and conceptual and mathematical underpinnings: We found that the model was well structured to achieve its purpose of estimating smolts that emigrate from the Tuolumne River as a function of the environmental conditions input into the model. The conceptual and mathematical underpinnings of the model generally appear to be sound and we have no issues with the major elements of these parts of the model. The scope of what is included in the model is quite extensive and we identified no issues with the components included in the model. Also, the actual structure of the model in how it was coded and executed also appears to be sound from our perspective.

Model complexity: The model is complex due to the individual-based framework that tracks individual fish through space and time in terms of fate, growth, and size. We found that initially it was difficult to alter different aspects of the inputs given the individual-based framework within the "R" statistical software package (R Development Core Team 2013). Fortunately, once we became familiar with the model, we were able to operate it to address our tasks, though altering certain inputs to address specific questions remained awkward and was time consuming.

Modeling documentation: The modeling report (Stillwater Sciences 2017a) is thorough and generally well written. However, due to the model's complexity, we found the report difficult to follow regarding the various connections of parts within the model and the interactions of those parts. On the whole, the documentation is well supported and referenced by relevant literature on salmon biology and ecology. The report would be aided by having a simpler summary of the model structure and key components, and diagrams of the different groups of fish being modeled and how each group contributes, or does not contribute, to estimated smolts produced per female spawner would be helpful.

The report is not as clear as it should be to indicate that the model is not a full life-cycle model. For example, Figure 3.0-1 is not relevant to understanding the model—the figure is easily taken to represent all of the life stages that are included in the model, which would imply that the model is a full life-cycle model. A more relevant figure showing what is included in the model and what is not included would be helpful for the reader. Similarly, Stillwater Sciences (2013a) includes sections on Delta rearing and outmigration (Section 5.2.5) and ocean rearing (5.2.6). While these components were discussed and reviewed during synthesis and therefore appeared to be judged as important at that time, these components of the life cycle are not included in the Chinook salmon model. This is confusing to a reader. The reason for not including these components and the model not being a complete life-cycle model should be clearly stated in the report. Even the name "population model" is a bit misleading. It is an in-river, smolt production model. The modeling report also would benefit by listing the different types of modeling outputs and how these outputs can inform management decisions.

The report authors do not discuss why they focus solely on smolt emigrants per female spawner and how this metric should be applied in guiding fish conservation and fisheries management decisions. The metric selected to express model results, smolt emigrants per female, does not provide the information needed to manage the river from either a conservation or a fisheries perspective. It appears designed to only address whether alternative "X" is better or worse than alternative "Y" in relative terms. While this is useful when comparing alternatives, the metric is not useful for informing how an alternative improves the intrinsic productivity or overall abundance of a stock because, in part, much of the production of the population is not included in the metric. Whether 6 or 17 smolts are produced per female is of little use to fishery or conservation managers because the values provide no information on the level of improvement in intrinsic productivity, nor on abundance, provided by the alternative or that is needed to stabilize, grow, or harvest the population. Because the model apparently is the management tool that will be used throughout the term of the license, the selected model output is not adequate for meeting conservation or fishery management needs.

Model transparency: The model structure and progression of modeled fish through the river is not sufficiently transparent to be useful, either to interested scientists or to managers. As noted above, the modeling report leaves out important explanations as to why some components of production are essentially ignored and why the metric emigrant smolts per female is the best and only metric of relevance. As a result, the model and its outputs are not sufficiently transparent to the reader to help understand the model, or to give guidance in applying modeling results. The primary drivers of the model are also not well identified and sufficiently discussed in Sections 5.3 and 6.0 of Stillwater Sciences (2017a). In particular, Figure 5.3-1 (page 5-9) is confusing and overly complex to easily follow—in fact, it is easy to misinterpret the charts. Moreover, the authors do not provide their criteria for how they determined which parameters were most important. We found Sections 5.3 and 6.0 of Stillwater Sciences (2017a), while helpful, to be muddled and inconsistent with regard to conclusions about the most important actions to take to improve the population performance of Chinook salmon. Also, in the Sensitivity Analyses section below we describe inconsistencies in results of sensitivity analyses that we observed, suggesting there are some errors in the calculations or in the assembly of results.

Model parameterization: We found that we might have applied somewhat different parameter values for some life-stage parameters, but after completing our evaluation of the model we concluded that other values we might have selected would have made little difference in the end. Also, as we note in Section 4.2 (Modeling Results), we found that certain survival rates that we computed using the modeling outputs were generally similar to rates applied in other Chinook salmon models that we are familiar with (e.g., the Ecosystem Diagnosis and Treatment model, see Blair et al. 2009, and a life-cycle model developed by NOAA Fisheries for a large river in southwestern Washington State, see Beechie et al. 2020). We also found that the number of smolts produced per female spawner (not emigrant smolts in this case) to generally be similar to Ecosystem Diagnosis and

Treatment modeling outputs for other basins we are familiar with, though somewhat lower, which is not surprising given the number of exotic predatory fishes in the Tuolumne River.

Life-cycle application: As we have noted several times, the model is not a full life-cycle model. It only models a single cohort of fish originating from a predefined number of spawners through their emigration from the river or their death. This means that the model cannot be used to evaluate whether the modeling scenarios are meaningful to the full life cycle of the species being modeled unless the modeler applies additional assumptions outside the model and conducts additional analysis. We were surprised that the report authors did not provide any discussion on this point to make it clear what the limitations of the model are and how it is meant to be applied to aid management. We discuss this further in the next section.

Calibration and validation: The investigators indicated that calibration and validation were conducted by comparing model results for fry and smolt production with annual production estimates available from the RSTs. Here, productivity means fry/female spawner and smolts/female spawner, not the intrinsic productivity of the population. Where they could, the investigators also used other data such as results from seining and snorkeling. Thus, there is a heavy reliance on the RST data and there were issues with these data that compromised calibration and validation as discussed in Section 4.1.1. Importantly, the investigators did not identify or describe the criteria they used to determine if the model was appropriately calibrated.

In Section 5.1 (Stillwater Sciences 2017a) the authors state that model calibration was accepted because the model predictions matched RST passage estimates for both fry and smolts at Grayson RST over a broad flow range. However, an examination of Table 5.1-1 and the associated figures (Stillwater Sciences 2017a) indicates the model performs poorly compared to data collected at the Waterford and Grayson RSTs. There is clearly an issue with the model predicting fry and smolts at the Waterford site. The model consistently overestimated the number of fry at Waterford and generally underestimated the number of smolts there. The differences between model and RST estimates of abundance are large. The model seemed to perform better at Grayson; however, there were still large differences here as well between modeled and estimated abundance, especially for fry.

The investigators note that the lack of model fit for smolts at Waterford may be due to model assumptions regarding fry movement and rearing locations. This may be a shortcoming of the model, but it also reflects potential issues with the RST data. Fundamentally, the model tracks fish through space (across reaches) and time. If the model is not predicting the number of fish at each check point in a reasonable manner, it suggests either shortcomings in the model or that the data used in the model has problems. Without having greater confidence in calibration, questions are raised about how well the model is characterizing limiting habitat conditions or limiting life stages.

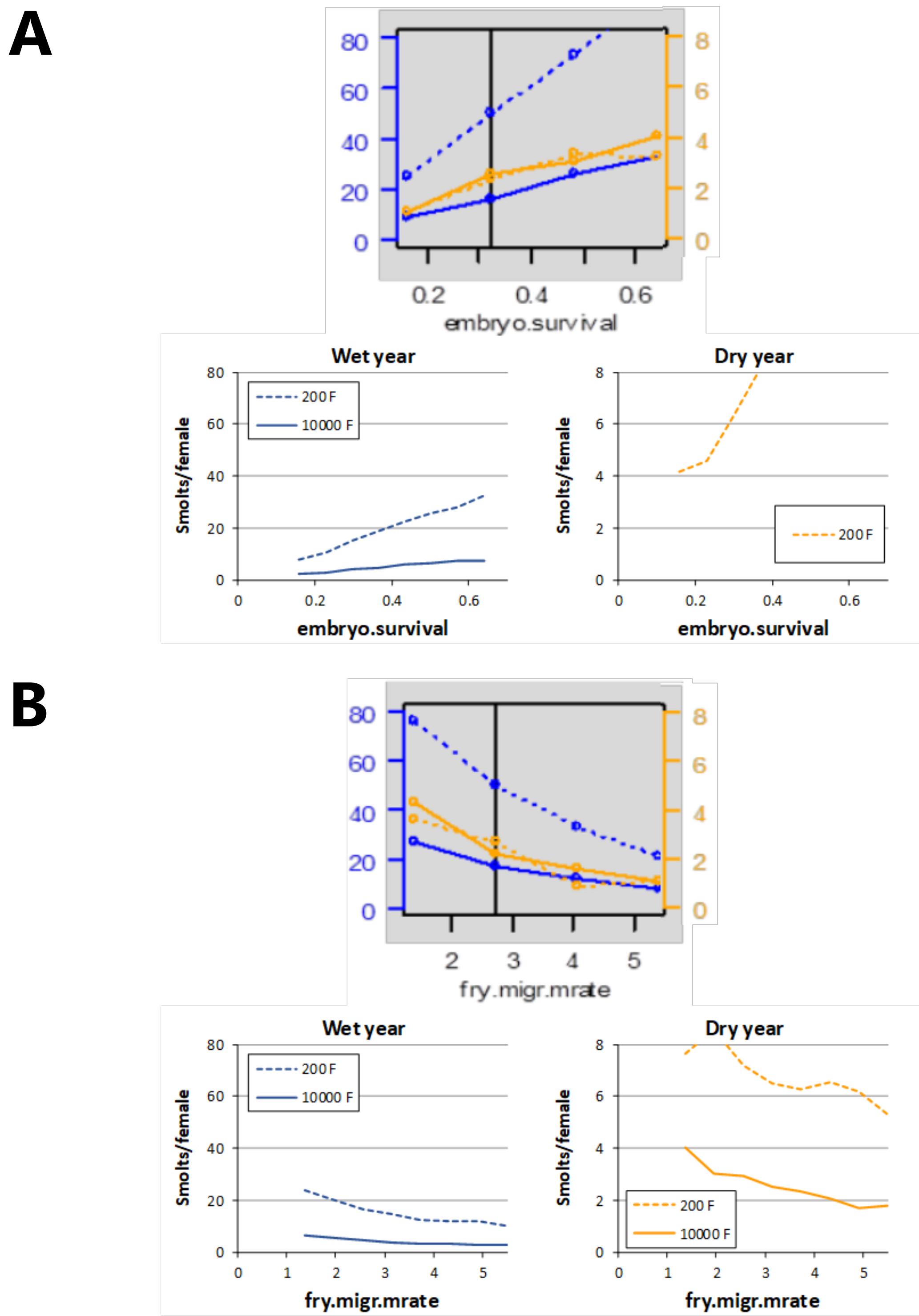
Sensitivity analyses: Sensitivity analysis is a critical part of model evaluation. The investigators did a considerable amount of sensitivity analysis, which is summarized in Figure 5.3-1 of Stillwater Sciences (2017a). Unfortunately, this figure is extremely difficult to interpret and it can be deceptive. Visually, the figure indicates that modeled productivities (smolts/female spawner) in Dry years fall between modeled productivities from high and low escapements in Wet years. In other words, it appears that modeled productivities in Dry years are higher than modeled productivities in high-escapement Wet years. However, this is not the case, as the investigators use two different Y-axes. Even though Dry-year productivities appear higher than modeled productivities from high escapements in Wet years, they are orders of magnitude different. Escapements in Dry years produce about 1 to 4 smolts/female spawner, while high escapements in Wet years produce about 10 to 40 smolts/female spawner (usually just under 20 smolts/female spawner). Although it is not readily apparent in the figures, Wet years, regardless of escapement size, produce nearly 10 to 20 times more smolts/female spawner than Dry years. Importantly, regardless of the specific value for a given parameter, Wet years consistently result in higher productivities than Dry years.

The investigators note that the slope of the productivity line was used to determine whether a given parameter was considered sensitive (i.e., sensitivity was assessed qualitatively by visual inspection to identify any slope deviations from horizontal in the sensitivity plots; see the response to Question 9 in Appendix A). It is not clear how steep (positive or negative) the slope needed to be for a given parameter to be considered sensitive. That is, there were no criteria identified for determining sensitivity. We would assume there are different criteria used to determine sensitivity for Wet years versus Dry years. For example, the greatest change in modeled productivities for Dry years over the range (minimum and maximum) of values evaluated is about three productivity units. Therefore, would a parameter that changes by, say, 2 productivity units over the range of parameter values evaluated be considered sensitive? It is unlikely this same rule would be applied to Wet years where productivities can vary by about 60 productivity units across the parameter values evaluated. Interestingly, the investigators did not identify embryo ultimate upper incipient lethal temperature as sensitive, even though productivity varied by 2 productivity units in Dry years and about 10 to 30 units in Wet years. In contrast, redd disturbance area was identified as sensitive even though the productivity change for Dry years was about 1 productivity unit and the change for the wet high-escapement scenario was about 10 units. We note that there was virtually no change in productivities for the wet low-escapement scenario. It appears to us that the identification of which parameters are sensitive may have been arbitrary.

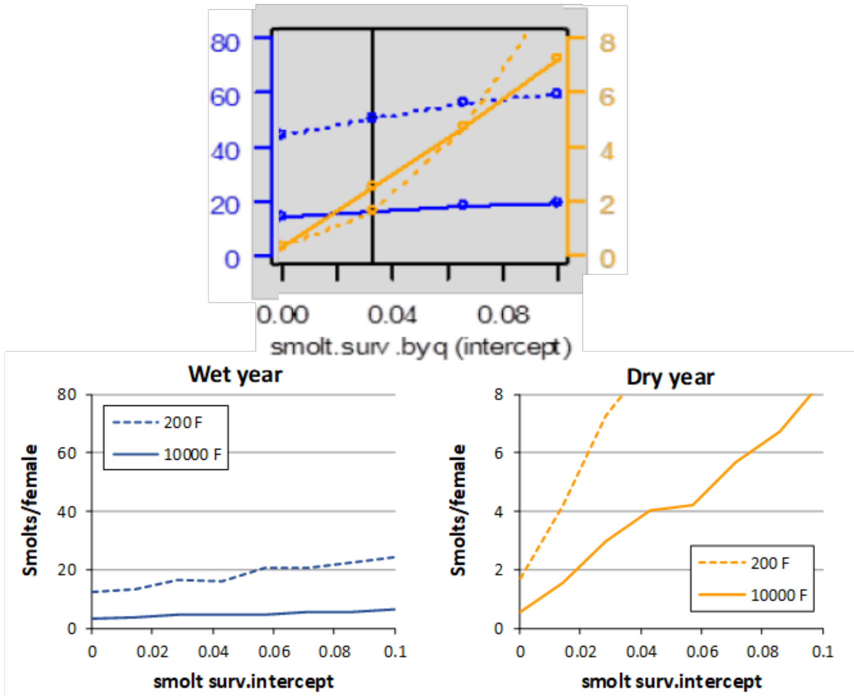
Due to the difficulty we had in evaluating Figure 5.3-1 in Stillwater Sciences (2017a), we requested that the raw modeling output be provided to us so we could reconstruct some of the graphs in a more conventional manner than had been done in the report (see Question 9 in Appendix A). The detailed data were provided to us in July, which we assembled and examined. We note that Stillwater Sciences stated in their response to us that "Note that because of the model coding error disclosed in the FERC filing of June 17, 2020 we have provided an updated compilation of model sensitivity testing results in the file Sensitivity TRCH33.xlsx (see FTP folder)." With regard to the nature of this coding error, the authors stated on page 1 of their memorandum that "The updated results included in the FTP reflect *small increases in smolt productivity* across all scenarios as noted in the June 17, 2020 FERC submission" (emphasis added by us).

The results of the updated sensitivity analysis provided to us have raised further, potentially more troubling questions that we cannot resolve. The results differ substantially from what had been displayed in Figure 5.3-1 of their report and are not consistent with their statement that there were "small increases in smolt productivity across all scenarios." To illustrate, Figure 11 compares the graphs from Figure 5.3-1 for four parameters considered in the sensitivity analysis to the results that we received in July. The four parameters, all of which were noted in the 2017 report as being sensitive in the model, are embryo.survival, fry.migr.mrate, and the intercept and slope parameters for smolt survival (smolt surv.intercept and smolt surv.slope). Figure 11 (A-D) compares each specific graph from Figure 5.3-1 in the report (shown at the top of each panel) for each of the four parameters to the model outputs sent to represent the updated results, which we re-graphed in a more easily understood manner. In each case, smolt productivities for the Wet WY are substantially <u>reduced</u> from those seen in the 2017 report and, in some cases, the patterns differ also. Results for the Dry WY are also substantially different. It is clear that there is some kind of error in either the 2017 report or in the data we received in July, other than the coding error that investigators noted in their memorandum. We are unable to resolve these discrepancies, which we believe are significant.

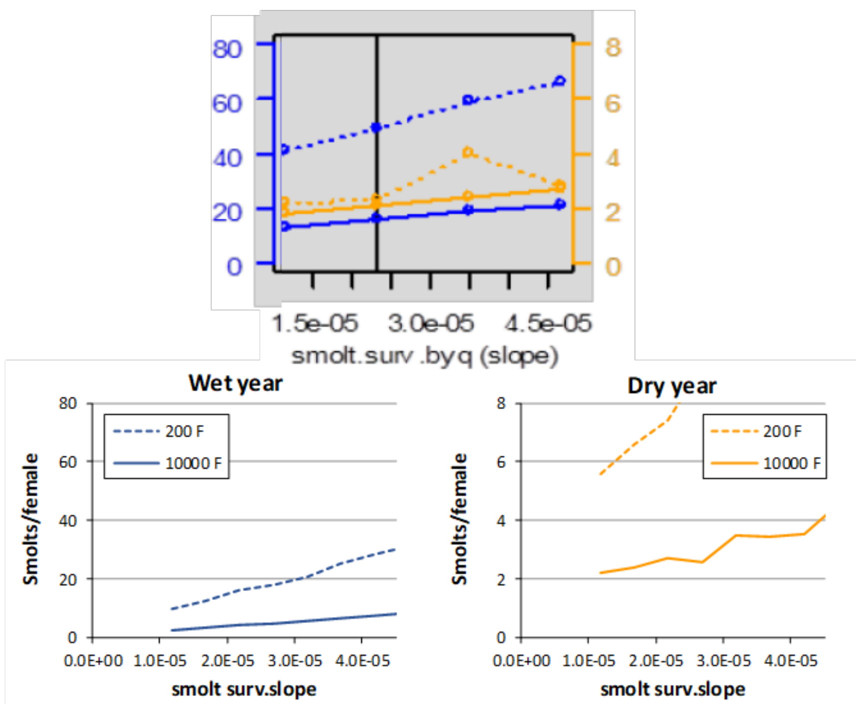
Figure 11
Comparison of sensitivity graphs.



C



D



Panels A-D compare sensitivity results at 200 and 10,000 female spawners (F) for four key model parameters presented in Stillwater Sciences (2017a) (upper plot in each panel) and based on data provided to Anchor QEA in July 2020 (see Appendix A) for Wet (lower left plot) and Dry (lower right plot) WYs.

4.2 Modeling Results

After reviewing the model's structure, its conceptual and mathematical underpinnings, parameters, and assumptions, we probed the model's performance to assess patterns of outcomes. We changed certain key parameters to assess or confirm effects on modeling outputs in a similar fashion as reported in Section 5.0 of Stillwater Sciences (2017a). This exercise was useful to better understand the results described in that report's sensitivity analysis. In Section 4.1.2, we discuss the inconsistencies in sensitivity results we observed in Sections 5.3 and 6.0 of Stillwater Sciences (2017a), which were inconsistent with regard to identifying the most important habitat drivers in the model and the implications for management actions given the current status of the population.

The model parameters that we focused on when running the model were survival from egg deposition to fry emergence (gravel.qual), survival of moving fry and juveniles (fry.migr.mrate and juv.migr.mrate), and smolt-to-smolt survival (smolt.surv.rstreach.byq). We expected that these parameters would directly affect the intrinsic productivity of the population, which is the population performance characteristic most important when a population is at low abundance or in a state of decline (Mobrand et al. 1997; McElhany et al. 2000), as it is in the Tuolumne River. Understanding intrinsic productivity also provides important information on the status of habitat quantity and the relative importance of density-dependence (i.e., is habitat quantity a limiting factor to the population in any life stage?).

To gain a clearer understanding on what the model (as configured) indicates about population performance for both intrinsic productivity and habitat capacity, we examined patterns of model output across the full range of spawner inputs available in the default model setup. The Chinook salmon model has been configured to easily model results at 100, 200, 1,000, 2,000, 5,000, and 10,000 female spawners. However, to ensure that we removed all effects of density dependence on the results, we also modeled scenarios with only 10 female spawners so results would not be affected by any habitat capacity limitations.

One of the issues Stillwater Sciences (2017a) suggests is affecting population performance is a limited amount of suitable spawning gravel, which purportedly leads to redd superimposition and reduced production of progeny. The report suggests that adding more spawning habitat through gravel augmentation would aid the Chinook salmon population (Section 6.3.1, page 6-3; Stillwater Sciences 2017a). We examined this issue by assessing population performance across a wide range of spawner abundances.

The model is configured to assess the effects of differences among WYs over a range of conditions. Datasets containing estimated daily average flow and water temperature for WYs 1971 to 2012 (42 years) at several locations along the Tuolumne River are included to be used as model inputs. These datasets provide a basis for assessing resultant population performance as predicted by the model in relation to both river flow and water temperature. We used the model to assess effects of these different environmental conditions on population performance over the range of spawners from 10 to 10,000 females.

We then examined patterns of population response for different population metrics, including numbers of emigrant fry, smolts produced (prior to initiation of smolt migration), emigrant smolts (smolts arriving at the Tuolumne River mouth), residual juveniles that continue to rear in the river after the smolt migration, as well as smolt-to-smolt survival and numbers of the fish in each of those categories produced per female spawner. We use the term "smolt-to-smolt survival" to mean the survival of smolts from the point of attaining smolt status (smolts produced) to the point of exiting the river at its mouth (identified as smolt emigrants in model output).

Each of these population metrics provides insights on how the Chinook salmon population responds to the range of environmental conditions experienced from the perspective of the model (i.e., given the model's design, assumptions, and data inputs). Models like this one are intended to provide insights on population responses to various environmental conditions that otherwise are often difficult to evaluate (Lee 1993; Scheuerell et al. 2006; Blair et al. 2009).

The model is structured to only assess a part of the life cycle of Chinook salmon, i.e., from spawner to smolt at the point of emigration out of the Tuolumne River. Neither the model itself nor the modeling report makes any attempt to present the results in a way to draw any conclusions about overall performance of the Tuolumne River Chinook salmon population, which is a serious limitation of both the model and the various related reports. Therefore, we considered possible implications of modeling results by incorporating factors outside the Tuolumne River using a range of simple assumptions about SARs (smolt-to-adult recruit survival). This exercise helped us evaluate whether the model produces reasonable results. We assumed different SAR values to estimate the number of adult recruits for the range of WYs being modeled, and then used conventional S-R analysis to estimate population performance metrics over the full life cycle, that is, for intrinsic productivity, habitat capacity, and equilibrium abundance.

4.2.1 Effects of Environmental Factors on Population Performance

The environmental factors that have the greatest effect on modeling results are those related to the RST data on smolt survival, particularly related to the model parameters identified as "fry.migr.mrate" and "smolt.surv.rstreach.byq." The RST smolt survival data, although it was intended to reflect only smolt-to-smolt survival, was also used to derive model parameter settings for survival of fry during movements downstream and for juveniles (prior to attaining smolt status) in their downstream movements. Modeling results are relatively insensitive to the juvenile migration mortality rate (juv.migr.mrate). Stillwater Sciences (2017a) attributed the cause of mortality during these three life stages (fry [following the initial emigration of newly emerged fry], juveniles, and smolts) during their movements to predation. Regardless of the exact cause, the low survival rates derived using the RST data are the most significant source of mortalities applied in the Chinook salmon model, and, in our opinion, it is the key driver of results in the model.

While the model has been configured to reflect an assumption that mortalities are greatest when either fry or smolts are moving downstream, the model demonstrates that flow levels passing the La Grange gage have a major effect to ameliorate mortality during fish movements, regardless of the number of spawners. The model suggests that the amount of flow during spring months passing this gage has the highest effect relative to other potential habitat factors on the following population metrics:

- Smolt-to-smolt survival (Figure 12)
- Total number of smolts emigrating from the river (Figure 13)
- Emigrant smolts produced per female spawner (Figure 14)
- Number of residual juveniles that continue to rear in the river following the smolt migration (Figure 15)

The relationship seen for smolt-to-smolt survival (Figure 12) is especially noteworthy. The smolt-to-smolt life stage is short and occurs without the smolts competing with each other for resources; hence, it directly affects intrinsic productivity for the population. The regression lines between April average flow and smolt-to-smolt survival are highly significant regardless of parent spawner abundance. Considering only this life stage, these modeling results suggest that intrinsic productivity for the population would be increased by a factor of about 21 times (or a factor of 16 times if the intercept in the relationship is set to 0) with an average April flow at La Grange gage of 8,000 cfs compared to a scenario with flow averaging only 500 cfs during that month. If the model is correct, then the relationship seen in Figure 12 provides clear guidance on a flow action that could be taken to dramatically increase intrinsic productivity of the population.[3]

[3] Density-independent survival rates among life stages in a salmon population are multiplicative, meaning that if you double the density-independent survival rate in one life stage, then the cumulative density-independent survival rate over the life cycle, that is, its intrinsic productivity, will also be doubled. See Mobrand et al. (1997) for a relevant discussion on the effects of changes in intrinsic productivity.

Figure 12
Smolt-to-smolt survival and average April flow at La Grange with different numbers of female spawners.

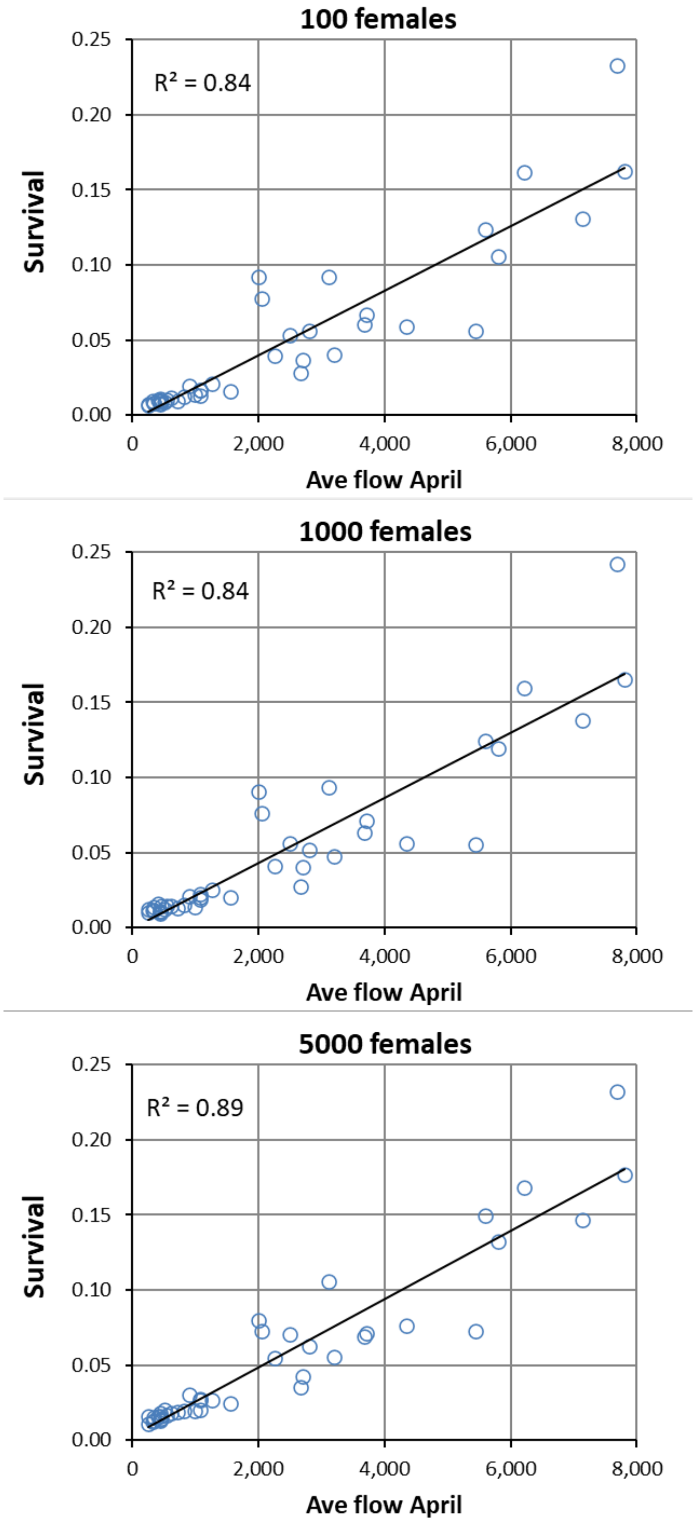


Figure 13
Total numbers of emigrant smolts and average April flow at La Grange with different numbers of female spawners.

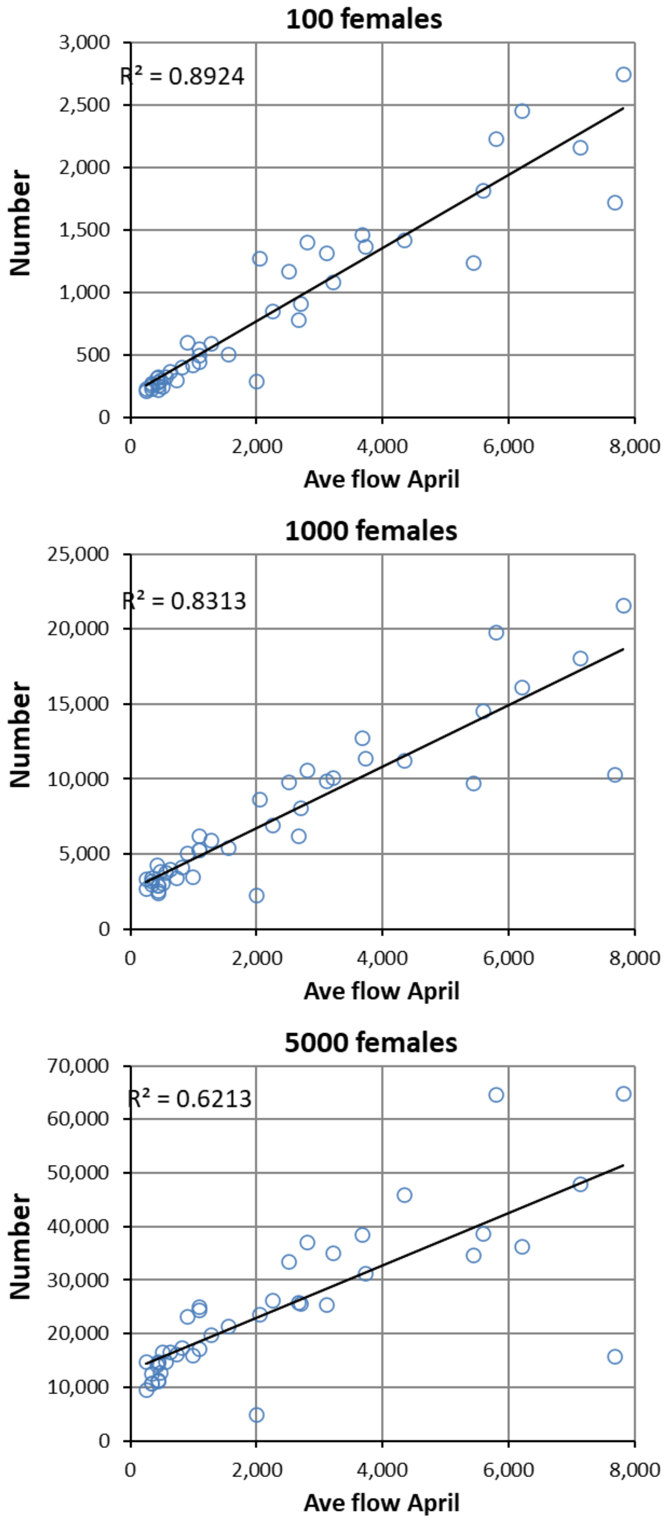
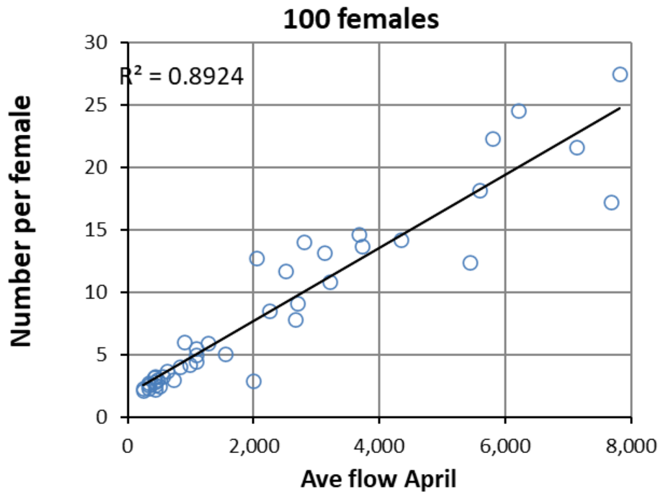
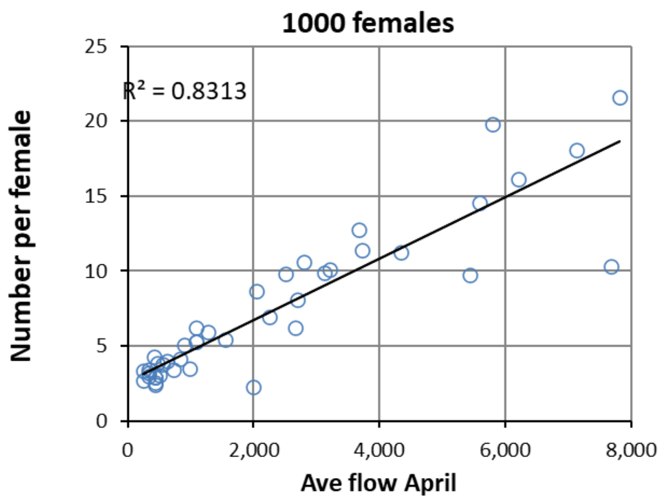


Figure 14
Numbers of emigrant smolts per female spawner and average April flow at La Grange with different numbers of female spawners.





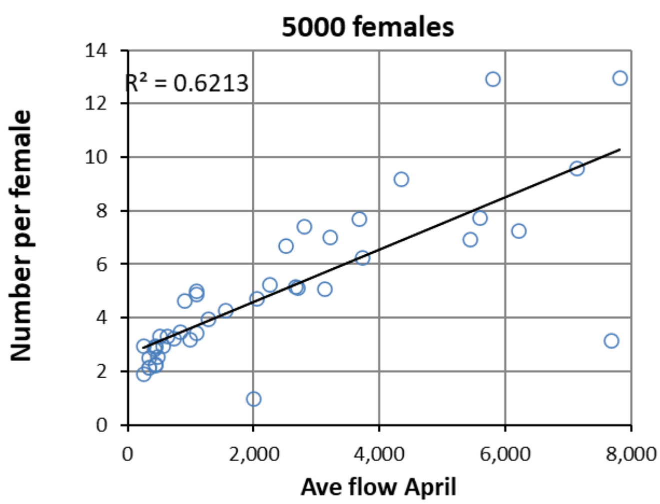
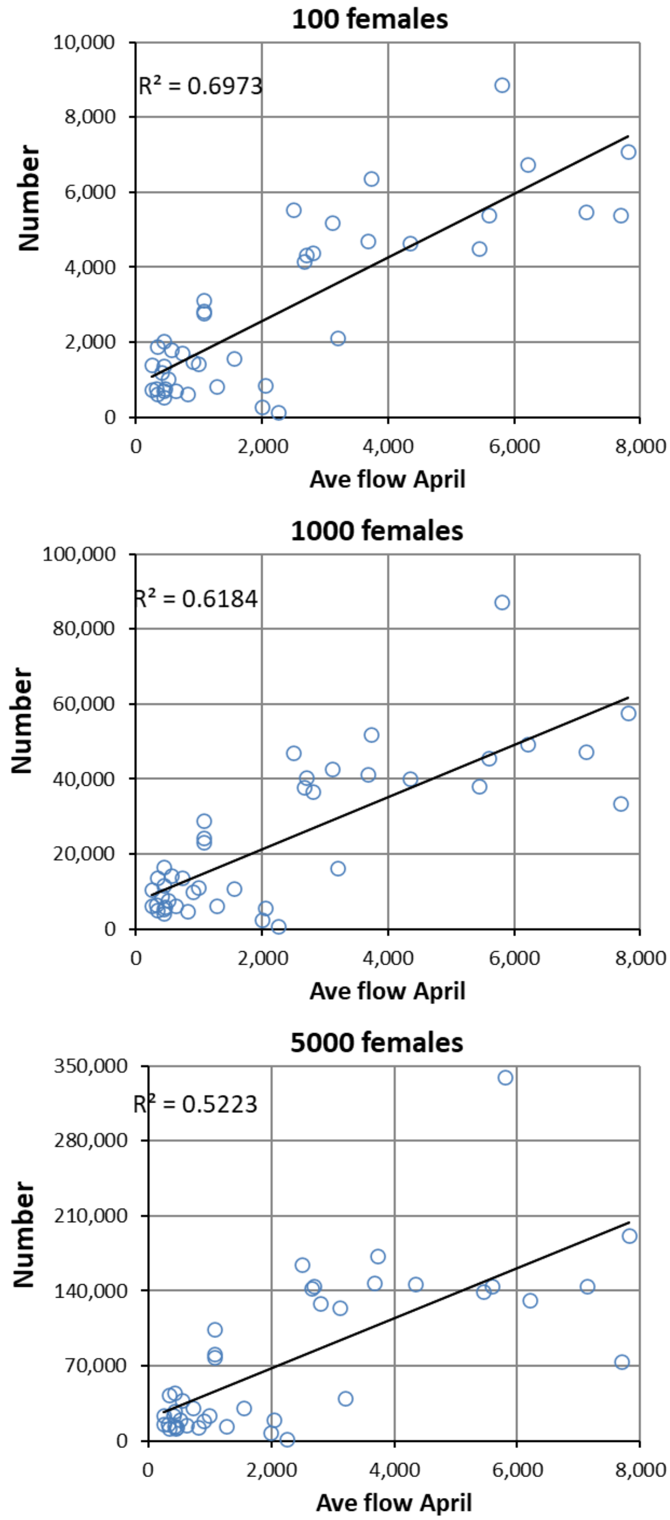
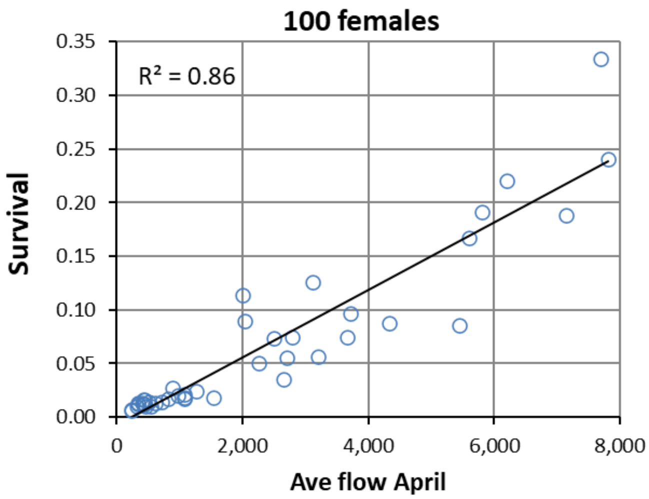


Figure 15
Total numbers of residual juveniles remaining to rear in the river following smolt migration and average April flows at La Grange.



As discussed in Section 4.1.1, we believe there is considerable uncertainty regarding the survival rate estimates derived from the RST data. We examined the effect of an increase in the slope parameter of the smolt-to-smolt survival relationship used in the model by increasing the slope to approximately match the higher regression line seen in Figure 9 of Appendix C in Stillwater Sciences (2017a) but did not change the intercept of the default regression line used in the model. The resultant relationship (Figure 16), if more accurate than the relationship with default settings in the model, would increase intrinsic productivity by a factor of about 30 times with an April flow average at La Grange of 8,000 cfs compared to an average of 500 cfs. The factor multiple would remain at 16 times if the intercept in Figure 16 is forced to be zero.

Figure 16
Smolt-to-smolt survival and average April flow at La Grange with 100 female spawners and applying an increased slope to the smolt survival relationship.



The relationships seen in Figures 13 through 15 need additional clarifying comments. These relationships are produced by WYs that consist of different ranges of conditions among months, of which April is only 1 month. The relationships seen in these three figures, while providing insights about the effects of flow in April, are more accurately interpreted to mean that if all months affecting fry, juveniles, and smolts had flow levels as seen in those WYs, then the predicted numbers of emigrant smolts would correspond to those in the figures. If the flows outside of April were different than those in WYs modeled, then the results would differ somewhat. However, the effect of smolt-to-smolt survival represented by Figure 12 would still apply; therefore, the overall patterns of those relationships are likely to still hold even if flows in other months were different.

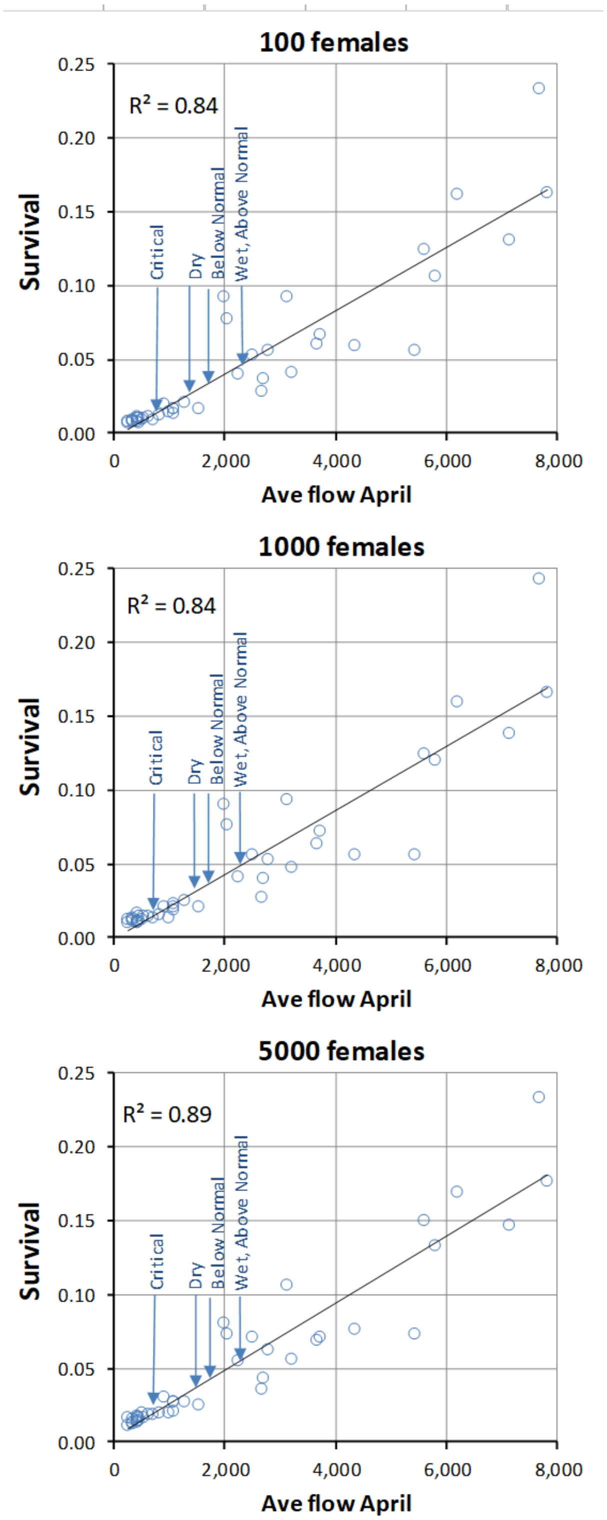
Also, the patterns seen in Figures 12 through 15 would remain essentially unaltered if one or both of the two other highly sensitive parameter settings in the model are changed (survival from egg deposition to fry emergence [gravel.qual] and the fry migration mortality rate [fry.migr.mrate]). While the model is quite sensitive to the assumptions made about those two parameter settings, reducing or increasing either one has little effect on the patterns seen in Figures 12 through 15 related to flows released during spring at La Grange Dam. The relationships depicted in Figures 12 through 15 are consistent with the findings of Mesick and Marston (2007) and Mesick et al. (2008).

Regarding Figure 15, as described under Section 4.1, the model reports the number of surviving Chinook salmon juveniles that do not smolt and are assumed to continue to rear in the river after the smolt migration ends. Ten percent of all fish that are eligible in the model to advance to smolt status are assumed to residualize and continue to rear. The investigators state that if these fish were to survive through summer and subsequently over winter in the river, that they could outmigrate as yearling smolts even though the model does not follow the fate of these fish. Moyle et al. (2017) states that the yearling life history is likely supported by the novel habitat conditions found in tailwater reaches below rim dams in California's Central Valley where fall Chinook salmon juveniles can potentially experience cool temperatures throughout the year at relatively low elevations. Figure 15 suggests that the number of juveniles that might residualize could be large (e.g., upwards of 40,000 or more when flows exceed 2,000 cfs during April). However, seining and snorkeling data summarized over a 10-year sampling period suggests that the abundance of juvenile Chinook salmon within the upper reaches of the lower Tuolumne River declines sharply after May of each year (TID/MID 2005). Snorkeling conducted in September of those years sampled suggests that few juvenile Chinook salmon remain in the river at that time. These observations suggest that the assumption in the model of a 10% residualization rate for smolt-sized fish may be high. If 10% of the fish residualize and are not moving, and thus have a low mortality rate based on the model and are rearing in cool water, then they should be observable in the empirical data. Therefore, the model does not seem to fit the empirical data. A high residualization rate for smolt-sized fish means that modeled estimates of the number of smolt emigrants from the river would be biased low. We point this out not to find fault, but to identify that further discussion of this aspect of the model seems warranted.

Finally, for context, Figure 17 relates the spring outmigration pulse flow schedule presented in Figure 2.2-1 of TID/MID (2019) that would occur under the "Interim Flow" schedule, to smolt-to-smolt survival and average April flow at the La Grange gage. Figure 17 shows the same model output used in Figure 12, but in addition it also indicates where the proposed flow regimes would occur on the regression of flow and smolt-to-smolt survival if the peak proposed flow occurred during the month of April.

Figure 17 is presented only to visualize where on the regression line the peak proposed pulse flow for each WY type would occur under different numbers of female spawners. It is important to recognize that daily average April flow in the figure, and for Figures 12 to 16 as well, is an average flow over the full 30 days of April. The data points in the figure are, therefore, the daily average flows for April for the 42 WYs in the record used in the model. The peak proposed pulse flows noted in Figure 17 that are from Figure 2.2-1 in TIM/MID (2019) are discrete values for a number of days associated with the proposed flow regime—they are not the average flows that would occur over the entire month of April. Hence, the two are not directly comparable and it would be incorrect to simply read from the figure what smolt-to-smolt survival would be under the "Interim Flow" regime for each WY type. However, Figure 17 provides a general reference for where the "Interim Flow" regime flows lie on the regression. The point we take away from the figure is that Critical, Dry, and Below Normal WYs land on the lower left-hand portion of the regression, and smolt-to-smolt survival as estimated by the model would be extremely low under these conditions.

Figure 17
Proposed peak pulse flows under the Interim Flow schedule by WY type plotted on the regression shown in Figure 12 (smolt-to-smolt survival and daily average April flow at the La Grange gage).



4.2.2 Relative Importance of Density-Independent and Density-Dependent Factors

We examined the relative importance of density-independent and density-dependent environmental factors by analyzing model outputs using conventional S-R methods. By doing so, we could consider the relative effects of how possible limitations in habitat quantity, regardless of life stage, affect population performance compared to environmental factors that operate strictly in a density-independent manner. Understanding the relative effects of density-independent and density-dependent environmental factors on population performance provides guidance on whether management actions should be directed mainly at issues involving habitat quality (e.g., associated with smolt-to-smolt survival, such as flows; this could also include predator control) or habitat quantity (such as gravel augmentation to increase the amount of suitable spawning habitat) or both factors.

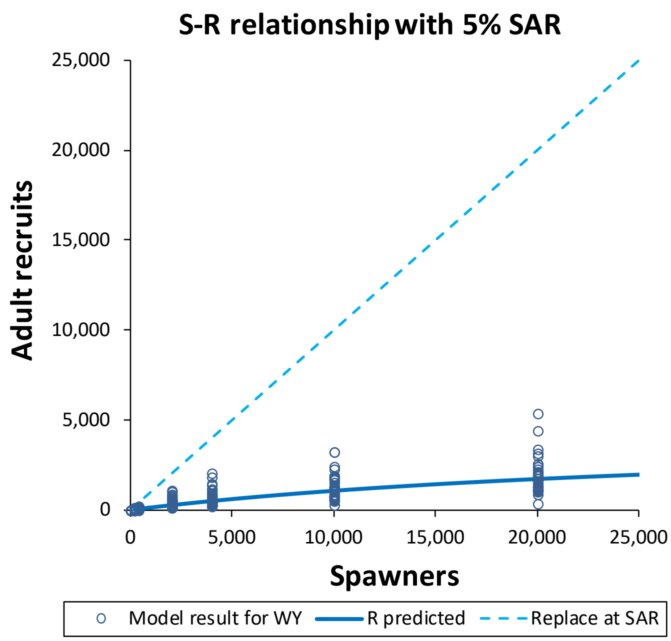
We estimated the number of adult recruits that would be produced from the modeled estimates of smolt emigrants leaving the Tuolumne River by assuming a range in SARs between 1% and 10%. We assumed the SARs to be constant over the 42 years of smolt emigrants estimated by the model. It is likely that the actual SARs experienced by Tuolumne Chinook salmon is generally closer to 1% or 2% than the higher values in that range, though on occasion it may spike much higher, even for consecutive years, when more favorable conditions occur. As a starting point, we applied an optimistic average SAR of 5% to illustrate the situation that exists for Tuolumne Chinook salmon as projected by the model.

Figure 18 displays a spawner-to-adult recruit plot using all 42 years of emigrant smolts with a fixed SAR of 5%. The numbers of spawners in the model that produced those recruits were 10, 100, 200, 1,000, 5,000, and 10,000 females. Total adult spawners were assumed to be twice the number of female spawners. We applied a maximum likelihood estimation method to estimate intrinsic productivity and capacity using a Beverton-Holt fit to the S-R data (Hilborn and Walters 1992). The plot clearly shows that all data points produced in this manner by the model fall well below the spawner replacement line. Intrinsic productivity needs to exceed a value of 1.0 for the S-R curve to pass above the replacement line to produce an equilibrium abundance >0; the estimated intrinsic productivity using all years of the data combined is 0.14. If all assumptions in the Tuolumne Chinook salmon model are correct, then the model suggests that the population has already been extirpated or it will be soon.

The actual condition of the population as suggested from the model would be worse than depicted in Figure 18 for two reasons. First, fishery harvest impacts were not incorporated, which would drive the intrinsic productivity even lower if recruits were evaluated at the spawning stage. Second, as discussed above the assumed SAR is likely too high and a lower assumed SAR would drive the intrinsic productivity value even lower.

These findings clearly illustrate that from the perspective of the model, intrinsic productivity is the issue primarily affecting population performance. Adding additional spawning habitat by gravel augmentation or adding any other aspect of habitat quantity would provide no meaningful benefit to the population in its current condition—the question of whether gravel augmentation would make sense at 5,000, 10,000, or more spawners is irrelevant. See Mobrand et al. (1997) for a useful discussion on the benefits of restoring habitat conditions that affect either intrinsic productivity or capacity under different situations. For Chinook salmon, the need from a population dynamics standpoint in the Tuolumne River is for habitat quality to be very significantly, and rapidly, improved. According to the model, the single factor that could dramatically improve intrinsic productivity would be to substantially increase flow releases during the smolt outmigration period.

Figure 18
Spawner-to-adult recruitment (S-R) relationship applying a 5% SAR to estimated numbers of emigrant smolts with default parameter settings in the model and different numbers of spawners.



4.2.3 *Spawning Habitat*

Stillwater Sciences (2017a) used PHABSIM modeling to quantify the amount of spawning habitat available at different flows within the river. Although there is a large body of literature that criticizes PHABSIM as a useful model for evaluating habitat availability, PHABSIM is commonly used to evaluate changes in habitat conditions with changing stream flows. Given our experience with PHABSIM modeling, we do not fault them for using PHABSIM in the Chinook salmon population model. However, we do question some of the suitability curves used to describe suitable spawning habitat for Chinook salmon. For example, Stillwater Sciences (2013b) converted criteria curves used in instream flow studies to a binary format, which means that over the range of environmental conditions, a metric is either suitable or not suitable. It does not allow for different degrees of suitability, which is found in the data on fish use that is used to develop the suitability curves. In addition, suitable depths for Chinook salmon spawning were set to range from 0.7 to 2.7 feet. This results in there being no suitable spawning habitat at depths greater than 2.7 feet.[4] We believe this is too restrictive given that Chinook salmon are known to spawn in areas up to 20 feet deep (e.g., Hanford Reach on the Columbia River). A review of the redd mapping reports and the spawning gravel study report (Stillwater Sciences 2013b) indicates that Chinook salmon spawned at depths greater than 2.7 feet in the Tuolumne River. It is therefore unclear why suitable depth curves were truncated at 2.7 feet. In addition, water depths, velocities, and substrate measurements were made at flows generally less than 200 cfs. If measurements were made at considerably higher flows, one may find even more Chinook salmon spawning at depths greater than 2.7 feet. We believe it is important to evaluate if the constraints placed on water depth have a large effect on total suitable spawning habitat.

PHABSIM modeling results, based on modeling spawning habitat at flows from about 50 to 1,200 cfs, suggest that spawning habitat is maximized at about 175 to 325 cfs among all survey reaches. It is unclear whether this would change if more reasonable spawning depth criteria are used to model suitable spawning habitat. It is also unclear if higher flows (>1,200 cfs) would have activated additional spawning habitat along the river. Unfortunately, the effects of flows greater than 1,200 cfs on spawning habitat were not evaluated by Stillwater Sciences (2017a).

For modeling the effects of gravel quality on egg survival, Stillwater Sciences (2017a) used an egg-to-fry survival of 32%, which appears to be based on work conducted in the Tuolumne River. This value is lower than the average of 44.6% reported in Quinn (2018) based on evaluating several published and unpublished studies. In contrast, the model used an egg-to-fry survival of 45% for *O. mykiss*. It is not clear why the rate used for *O. mykiss* is considerably greater than the rate used for Chinook salmon, given that both species use essentially the same spawning areas. In addition, gravel augmentation is modeled by increasing the egg-to-fry survival rate from 32% for Chinook salmon under existing conditions to 50% under gravel augmentation conditions (TID/MID 2019). It is unclear why this value was chosen or if it reflects reality under a gravel augmentation scenario.

[4] Interestingly, the PHABSIM report compared steelhead spawning habitat (WUA) using depth-limited (a defined maximum depth) and depth-unlimited (no maximum depth) suitability curves. Resulting WUA for spawning habitat differed considerably depending on which curve was used. In general, using the unlimited-depth curve generated greater estimates of WUA than using the depth-limited curve. We believe an unlimited-depth curve should have been used to model Chinook salmon spawning habitat.

As described in the redd mapping reports, some level of redd overlap occurs at most Chinook salmon spawning escapements, and the incidence of redd overlap increases with escapement. However, the level of egg mortality associated with redd overlap was not quantified. Rather, it was assumed that the level of egg mortality was proportional to the degree of redd overlap. In other words, if 10% of a given redd was disturbed by a later spawning female, then egg mortality in the model was also assumed to be 10%. We found no justification for this assumption presented in the Stillwater Sciences reports. Often, Chinook salmon redds can overlap with little or no loss of eggs. This is because eggs are not deposited evenly throughout the area of a given redd. Instead, eggs are deposited in one or more egg pockets located within the disturbed area of the redd. Only when a later arriving female digs up an egg pocket will there be some level of mortality.

For Chinook salmon, the degree of redd superimposition is a function of (among other things) redd defense time by female spawners. The longer a female defends her redd following spawning, the less likely another female will spawn on top of her redd. Stillwater Sciences (2017a) noted that typical redd defense times can range from 6 to 25 days. For modeling purposes, a redd defense time of 7 days was selected, which is near the minimum number of days reported in the literature. For sensitivity analysis, a range of 4 to 14 days was evaluated. Redd studies conducted on the Tuolumne River in 1988 and 1989 are cited as the basis for selecting a 7-day redd defense time as the "typical" value. It is not clear why then 4 to 14 days were selected for sensitivity analysis. Because female defense reduces redd superimposition, using a short redd defense time will lead to greater redd superimposition in the model and therefore lower egg-to-fry survival. In addition, egg-pocket depth is related to fish size. If the first female is larger than the second female, there could be complete redd overlap with few of the eggs from the first female lost, because they were buried deeper than the egg pockets constructed by the second female. Quinn (2018) notes that in general, late-arriving females tend to be smaller than earlier arrivals.

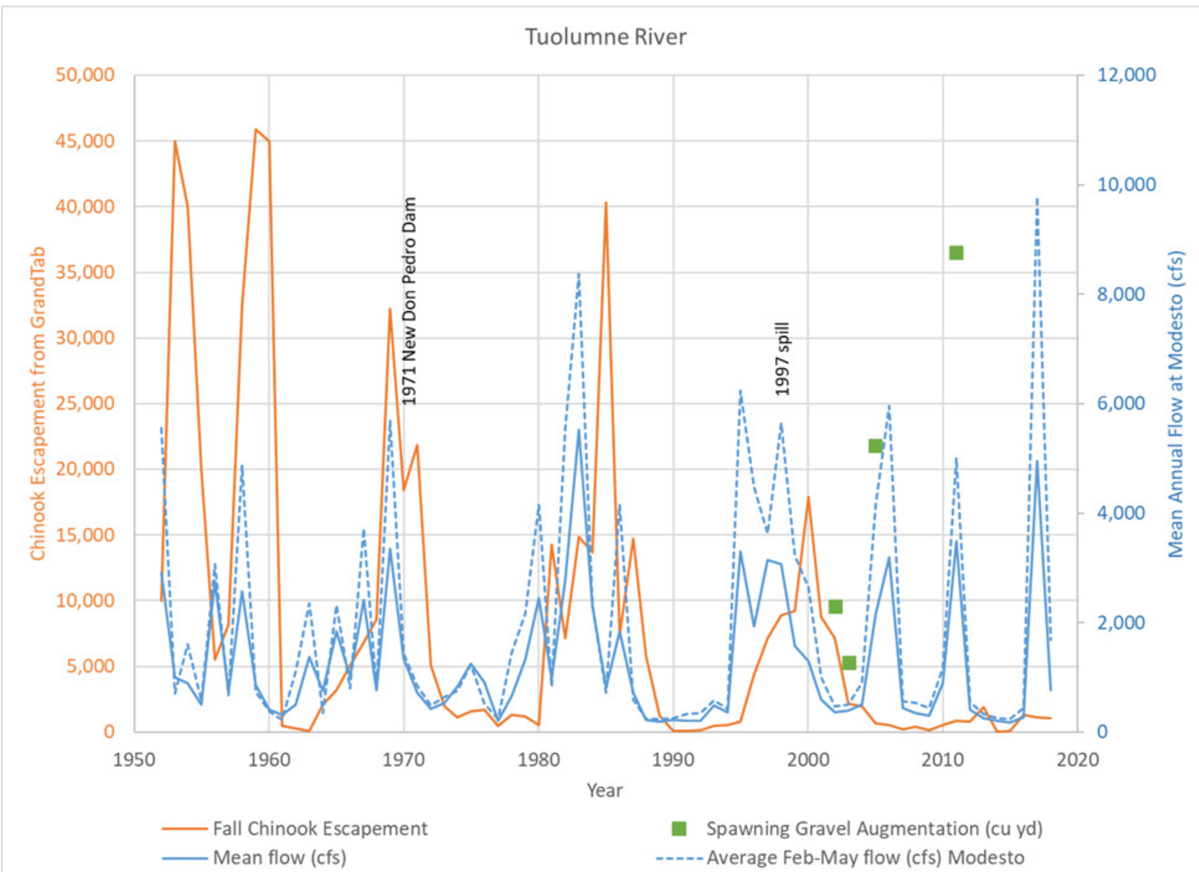
Stillwater Sciences (2017a) suggested that measures to improve spawning habitat would result in proportionate increases in juvenile Chinook salmon production. Although we generally agree that improved spawning habitat quality would improve intrinsic productivity of the population, we believe the gain in intrinsic productivity from gravel augmentation and gravel cleaning is relatively small compared to improving flows during smolt migration (see Section 4.2.2). Currently, spawning gravels in the river could support an escapement of 48,000 to 60,000 Chinook salmon depending on flows (Stillwater Sciences 2013b).[5] Compared to the highest reported escapement since 1960 (approximately 40,000 Chinook salmon in the mid-1980s), there appears to be adequate spawning habitat available for Chinook salmon in the Tuolumne River. Based on Stillwater Sciences (2013b), there was perhaps a 15% loss of spawning gravels during high flows encountered in 1997, but with

[5] For comparison, the same study indicated that available gravels could support an escapement of 803,000 to 855,000 *O. mykiss*.

recent gravel augmentation, there should still be more than adequate spawning gravel available to support both current and high escapement levels.

From a life-cycle perspective, the 2002 to 2011 gravel augmentation work did not translate into an observable increase in adult escapement based on visually relating gravel augmentation to patterns in spawning escapement (Figure 19). Escapements through 2004 appear to be related more to mean flow from the year the returning fish spawned than to gravel availability. After 2004, escapement levels have been low and did not increase despite gravel augmentation in 2002, 2003, 2005, and 2011. Therefore, based on a review of the available literature and visual interpretation of Figure 19, gravel augmentation does not appear to translate into more spawners. This appears to be in contrast with results from the Chinook salmon model, which only estimates production of smolts. We believe spawning gravels currently available should be sufficient to support escapement levels of more than 40,000 fish.

Figure 19
Chinook salmon escapement, mean flow, and spawning gravel augmentation in the Tuolumne River, 1952 to 2018.



Data from GrandTab (compiled 5/7/2019), USGS gage data, and Stillwater 2013a

As noted above, scenario modeling conducted by TID/MID (2019) suggests that gravel augmentation and/or gravel cleaning would increase production of Chinook salmon smolts. However, results of modeling we conducted using the Chinook salmon population model indicates that smolt-to-smolt survival strongly affects the intrinsic productivity of Chinook salmon in the Tuolumne River. That is, the largest determinant of intrinsic productivity, according to the model, is the period between when smolts are produced within the river and when they exit the river (see Section 4.2.1). The model predicts that the numbers of fry and juveniles produced by the river would likely be sufficient to sustain the population if smolt-to-smolt survival was significantly higher than what is applied in the model and if SAR was in the neighborhood of 2%. Spawning habitat does not appear to be limiting population performance in any meaningful way. Similarly, the quantity of rearing habitat for fry and juveniles (parr) is also not limiting population performance in any meaningful way. We note, however, that any improvements that could be made in the *quality* of spawning, incubation, fry, and juvenile habitat would increase the overall intrinsic productivity of the population.

4.2.4 Juvenile Rearing Habitat

The Chinook salmon population model is being used to evaluate rearing habitat and its effects on smolt productivity. We evaluated how the model estimates rearing habitat by reviewing assumptions and model predictions.

Stillwater Sciences (2017a) used PHABSIM modeling to estimate changes in Chinook salmon fry and juvenile rearing habitat associated with changes in stream flows. As was discussed in Section 4.2.3, we do not fault the researchers for using PHABSIM in the population model. We appreciate that fry and juvenile salmon habitat was quantified at flows that inundate floodplain habitat.

PHABSIM modeling indicates that there are large gains in fry and juvenile habitat at flows greater than 1,200 cfs. For Chinook salmon, maximum usable fry and juvenile habitat appears to exist at 3,000 to 4,000 cfs. Although there is a clear relationship between flows and rearing habitat for fry and juvenile Chinook salmon, Stillwater Sciences (2017a) appear to downplay the large gains by noting that the 2D-model-derived estimates at the site scale may not represent all conditions occurring river wide. That is, they note that the estimates for the reach downstream of Shiloh Bridge (RM 3.5) may be influenced strongly by backwater effects from flood flow conditions occurring in the San Joaquin River (Stillwater Sciences 2017a). However, even if the lowest reach (Shiloh Bridge to mouth) is removed from the weighted usable area (WUA) analyses, there remain large increases in usable habitat for fry and juvenile Chinook salmon at higher flows. The researchers also note that the proportion of usable fry and juvenile habitat to area inundated for Chinook salmon decreases with increased floodplain inundation. We suggest that the proportion is not important to fish. Rather, the total increase in usable habitat is important to fish, and the results indicate a clear and large increase in usable fry and juvenile habitat with increased flows. We also point out that not only is there more usable fry and juvenile habitat at higher flows, there will be less predation on fry and juveniles at higher flows. That is, predation risk decreases with flows as floodplain inundation occurs because predators feed more effectively in-channel than on inundated floodplains and along banks, as is noted in Attachment A of Stillwater Sciences (2017a).

Chinook salmon model results indicate that fry are displaced (move downstream and are captured in RSTs) during high-escapement years and wetter years. Because these fish move out of the Tuolumne River, these fish are no longer included in the model. As discussed in Section 4.1, in terms of the model, these fish do not contribute to estimated productivity (i.e., they are considered dead). In reality, this may not be the case. Some of these fish may survive to smolt outside the Tuolumne River. Indeed, many may survive and recruit to spawners, and their survival outside the Tuolumne River may be related to flow. That is, higher stream flows in the Tuolumne River may increase their survival rate outside the Tuolumne River if inundated floodplain habitat is available downstream from the Tuolumne River. Thus, there could be a survival benefit associated with higher Tuolumne River flows that is not captured in the model because the model is only focused on survival within the Tuolumne River.

There is a potentially important interaction between flow and predation that the model appears to be missing. Anytime a Chinook salmon fry is moving (displaced or otherwise), the model applies a "migration mortality" rate for as long as the fry are moving (fry.migr.mrate). The assumption made in the model is that moving fry and juveniles are subject to predation losses. However, displacement is also likely correlated positively with flow, and predation is likely correlated inversely with flow. Thus, during higher flows, more fish may be displaced, and they may experience lower predation rates as a result. As far as we can tell, the model does not incorporate any interaction of flow, potential displacement, and predation in this manner.

Stillwater Sciences (2017a) states that juvenile emigration prior to smoltification is not assumed to occur. We requested clarification of this and the Chinook salmon model does simulate low levels of parr emigration by drift and through displacement at higher densities (see Attachment A). We were glad to hear this because ocean-type Chinook salmon (summer and fall Chinook salmon) tend to "rear-on-the-run." That is, they consistently move downstream during rearing. Also, results of otolith analyses clearly indicate that juvenile Chinook salmon emigrate before smoltification, where 40% to 73% of the adult Chinook salmon that returned to the Tuolumne River and were sampled had exited the river as parr (Table 6, Appendix A; Stillwater Sciences 2016).

Productivity in terms of smolts per female spawner (not intrinsic productivity) was selected as the response variable when evaluating the effects of various treatment/management actions (e.g., increases in flows, gravel augmentation, floodplain inundation, predator removal) (TID/MID 2019). However, Table 6 of Appendix A in Stillwater Sciences (2016) indicates that all size classes of juvenile outmigrants were represented in the adult spawning population for juveniles that outmigrated in the 5 years evaluated between 1998 and 2009. Tuolumne-origin adults were composed primarily of individuals that emigrated from the river as parr and smolts; however, in outmigration year 2000, 20% of the returning adults had outmigrated as fry (Table 6). Consistent with observations of other populations in the San Joaquin Basin, parr outmigrants were generally the most commonly observed phenotype in the returning adults, implying a potential survival advantage despite being smaller than smolts (Stillwater Sciences 2016). Based on Table 6 in Appendix A of Stillwater Sciences (2016), smolts comprised from 8% to 60% of the adults, or, in other words, the contribution of fry and parr together to adult returns ranged from 40% to 92% among the 5 years sampled.

Because the model truncates the spatial scale of the analysis to the Tuolumne River and because otolith analysis indicates that large numbers of spawners smolted outside the Tuolumne River, the current modeling approach does not capture the “true” number of smolts per female for females that spawn within the Tuolumne River. Given that a large proportion of juveniles leave the Tuolumne River as fry or parr and return as spawners, and there is a relationship between flow and fish emigrating from the Tuolumne River, increased flow would increase the productivity of Chinook salmon associated with water management alternatives if “all” smolts produced are included in the model. Thus, by restricting the spatial scale of the analysis to the Tuolumne River, the model cannot accurately predict the number of smolts per female produced as a result of different management scenarios. As discussed in Section 4.2.1, while relative differences between water management alternatives are informative, the more important metric in terms of understanding whether productivity is sufficient to support the population is total smolts produced from the entire suite of Chinook salmon life histories. Thus, as constructed, we do not believe the Chinook salmon population model fully achieves the guidance from FERC that it address the “population response for specific in-river life-stages including smolts for existing conditions and for potential future conditions” (Stillwater Sciences 2017a,b). Also, the model could, but was not used to evaluate future changes in hydrology and temperature associated with climate change as described in Section 6.2. Thus, changes in juvenile rearing habitat associated with future climate regimes were not assessed or incorporated into model results.

Although we identified some issues with the model and its assumptions (as noted above), the results suggest there is more usable habitat and higher survivals for fry and juvenile Chinook salmon at higher flows (>1,200 cfs). Even though this is downplayed in the Stillwater Sciences (2017a) report, the relationships appear quite strong. However, an increase in the quantity of usable habitat will likely not significantly increase fry and juvenile survival, and therefore, would likely not improve Chinook salmon intrinsic productivity unless floodplain inundation was substantial enough to provide access to higher quality food resources for rearing juveniles.

4.2.5 Water Temperature

Water temperature is a key environmental variable and critical limiting factor for salmonid survival and productivity. We evaluated this concern by examining how temperature is incorporated into the population models and model predictions. As presented in Section 4.2.1, modeling results indicate that spring flows are likely the major driver of smolt-to-smolt survival of Chinook salmon, as well as the number of smolt emigrants that exit the lower Tuolumne River. This pattern of response by Chinook salmon to flows is consistent with previous analyses reported by Mesick and Marston (2007) and Mesick et al. (2008). We note, however, that flows during the spring and summer are also highly correlated with temperatures during the warmest months of summer, namely June to August, but the Chinook salmon smolt migration past the Grayson RST (RM 3.5) is largely over by the end of May (Stillwater Sciences 2017a). Therefore, we find that it is unlikely that the mechanism for increased smolt-to-smolt survival in relation to spring flow is due to reduced water temperatures as a result of higher flows. However, in years of prolonged low flows during spring, elevated water temperatures during the smolt outmigration may be an issue affecting survival, particularly during May. We would expect that this situation will worsen with climate change. The solution in any case for realizing increased smolt-to-smolt survival is to maintain high flows to the extent feasible during the smolt migration, which would serve to keep the river cooler as well as to reduce predation. We also note that in Wet years with high spring runoff, water temperature can remain cooler into June, which also tends to prolong the smolt migration, which is demonstrated in Figure 5.4-3 of Stillwater Sciences (2017a).

4.2.6 High Priority Assigned to Predation and the Effectiveness of the Districts' Proposed Suppression Methods

It is quite likely predation is the reason for the poor smolt-to-smolt survival within the Tuolumne River. It seems reasonable, therefore, to try and reduce predation effects during the period when smolts migrate out of the river. We recognize the comments provided by CDFW (CDFW 2020) questioning the effectiveness of predator removal actions and potential uncertainties associated with these actions and the Districts' response (TID/MID 2020b). Our conclusion on this topic is that while predation effects are estimated to be large, the Chinook salmon production model cannot tell us the number of predators or how much suppression is needed to achieve a significant increase in smolt-to-smolt survival. On the other hand, and more importantly, the model can predict changes in smolt-to-smolt survival with stream flows. That is, as discussed in Section 4.2.1, the model demonstrates a clear and positive relationship between mean April flows and smolt-to-smolt survival in the Tuolumne River. For example, the model predicts a smolt-to-smolt survival rate increase from 0.01 at 300 cfs to nearly 0.15 at 8,000 cfs (survival is even higher at 9,000 cfs). That equates to a 15-fold increase in survival with a 27-fold increase in mean April flows. The model assumes an indirect relationship between flow and predation mortality (i.e., the model assumes smolts have lower mortality rates at higher flows because the higher flows move the smolts through the river faster and therefore there is less time for predators to prey upon smolts), but it cannot tell us with any certainty the amount of predator suppression needed to achieve a 15-fold increase in smolt-to-smolt survival.

Verification of whether an assumed change in mortality from predator control will occur will require experimentation, for all the reasons identified in CDFW (2020), and perhaps using an adaptive management approach as TID/MID (2020b) indicates is being considered. Our conclusion is that although it may be important to remove or suppress predators, especially non-native predators, there is no certainty that predator removal or suppression will significantly increase the intrinsic productivity of the Chinook salmon population. However, there is much more certainty, based on model predictions, that increasing flows during smolt migration will increase smolt survival and escapement.

4.3 Model Conclusions

The Chinook salmon population model is a useful tool for helping to evaluate the production of emigrant Chinook salmon smolts in the Tuolumne River in relation to habitat conditions, including flow regimes and predation effects. The model can provide important insights to scientists and managers alike about the status of the population and factors affecting population performance. More specifically, we found that it appears to have utility to help diagnose the effects of various conditions threatening population performance and identify and evaluate management actions that can improve performance.

We found that the model is designed, structured, and parameterized to be useful in addressing basic questions related to the number of emigrant smolts that would result from specified numbers of spawners under different flow and temperature regimes. In general, we found that the model's conceptual design is well supported and documented—although we also found that the model and its documentation are not sufficiently clear and transparent to be useful to all readers.

Based on our review and analysis, we conclude that the model indicates that the Chinook salmon population is most threatened by extremely low intrinsic productivity. This means that the population is being most adversely affected by habitat quality, which would include the effects of predator populations. A shortage of habitat quantity, including spawning habitat and gravel availability, is not a limitation on the population at abundance levels that are of concern. Gravel augmentation would not be expected to improve population performance in any measurable way. Similarly, increasing flow during spawning to increase available spawning habitat would likely have only small or negligible effects on the population.

The model, as configured, indicates that the status of the Chinook salmon population is extremely precarious and bold actions are required to prevent extirpation. This need, according to the model, would best be met by very substantial increases in flow releases during spring (the period of active smolt outmigration from the river). Other actions that might result in reductions in predation rates, unless those reductions could be of a significant magnitude, or increases in spawning habitat, even if those increases were large (e.g., by gravel augmentation), could be expected to provide little benefit by comparison to flow increases. The model suggests that management actions with the most certainty in providing real benefits would involve increases in flows during smolt outmigration.

Despite being useful, the model has a number of shortcomings. Foremost, the model is not a full life cycle, which hampers its utility for evaluating potential benefits of management actions to the overall population. The model also does not account for population components other than fish that smolt while in the river that also contribute to overall adult production. Fry migrants (newly emerged fry), slightly older fry emigrants, juvenile emigrants prior to smolting, as well as juveniles that residualize and continue to rear in the river, are treated as mortalities in terms of their contribution to population productivity. In this regard, the model has a very narrow scope that omits important life histories that contribute to the population based on analysis of otoliths. While the model can be used to inform relative differences between management alternatives without including these life history expressions, the assessment will be incomplete without considering how the entire population responds to the actions, and thus falls short of meeting the guidance provided by FERC in our view. In addition, and because of this, from our perspective the Chinook salmon population model as configured is inadequate for managing the Chinook salmon population for conservation or fisheries over the term of a FERC license because it does not inform surplus over replacement, as discussed in Section 2.4. It is an in-river smolt production model using preset spawner inputs, not a population life-cycle model.

Uncertainties exist with the model, particularly with regard to parameters related to predation effects. Estimates of mortality during the smolt-to-smolt life stage based on the RST studies are the largest driver of the results produced from the model. We found the model did not calibrate well to observed smolts arriving at the Waterford RST, which brings into question its ability to estimate life-stage transitions and survival to this sampling location. The relationship between flow and survival based on the RST data can take several forms, all of which appeared to incorporate a high degree of variability in the data at certain flow levels. We believe there is a need to improve the estimates of smolt-to-smolt survival if the model is to be used for evaluating management alternatives. At the very least there is a need to increase confidence in the estimates of smolt-to-smolt survival and in the relationships between survival and flow developed based on the estimates.

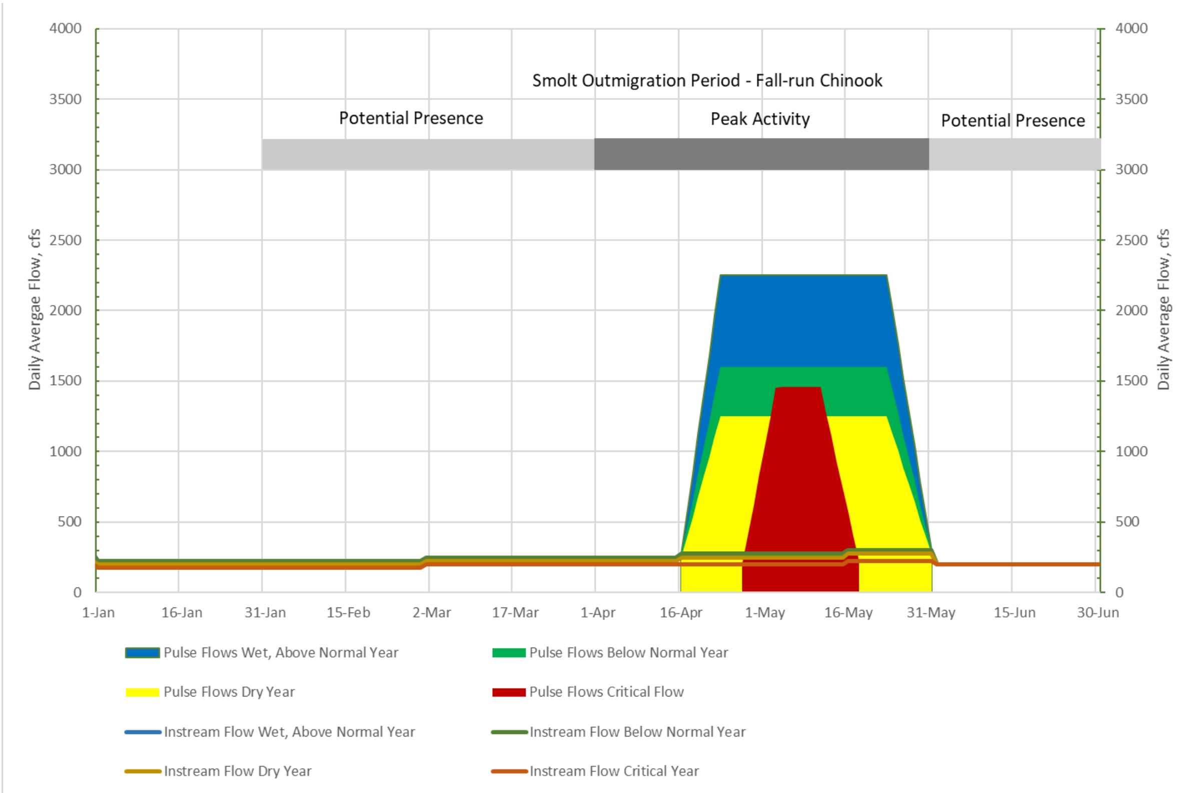
The Chinook salmon population model is not easy to use. From our perspective and the assumption that this is the river and fisheries management tool that will be used for the term of the FERC license, the Districts should make the Chinook salmon model available to stakeholders (if they have not already done so), and the stakeholders need to learn how to operate the model and fully understand its limitations. Model users would benefit by having the model developers incorporate model features to make it easier to evaluate customized water management scenarios such as a user-friendly interface like Shiny (an R package for developing interactive web applications).[6]

Flow volume is limited and stakeholders should use the model to explore tradeoffs among 1) winter flow augmentation to displace fry downstream (knowing that displaced fry in the model do not contribute to smolt-to-smolt survival but do return as adults based on otolith analysis); 2) winter flow augmentation for rearing (Mesick and Marsten [2007] found early rearing flows during March and possibly February to be particularly important factors controlling adult recruitment in the San Joaquin River Basin as adult recruitment was highly correlated with the number of smolt-sized outmigrants that emigrated from the Tuolumne River); 3) spring pulse flows during April and May as proposed by the Districts; and 4) the value of fall pulse flows for adult attraction based on Peterson et al. (2017).

Regarding the spring pulse flows during April and May, proposed flows relative to the Chinook salmon smolt outmigration period as defined in Table 5.2-1 of Stillwater Sciences (2013a) are presented in Figure 20. The figure clearly displays how the proposed flow regime does not extend long enough to cover the full outmigration period, which suggests that life history diversity that is so important to Chinook salmon production is not being supported. Regarding assessing the value of fall pulse flows, Peterson et al. (2017) reported that managed pulse flows during fall resulted in immediate increases in daily passages of adult Chinook salmon, but the response was brief and represented a small portion of the total run. They observed a strong nonlinear response between migratory activity and discharge levels, indicating no additional increase in daily counts when pulse flows exceeded 705 cfs. The potential for applying these findings to the Tuolumne River needs additional analysis and discussion.

[6] The model currently uses Shiny for a user-interface, but the feature is limited in how it is applied.

Figure 20
Proposed flow regime for the Lower Tuolumne River compared to the Chinook salmon smolt outmigration period.



Finally, a modeling report should be prepared that provides greater clarity and transparency for how the model is structured and operated with clear and concise instructions for application. Modeling results need to be presented in a manner that provides clear guidance on interpreting model outputs for application to management. These aspects of the model should be developed in collaboration with stakeholders and potential users.

5 Oncorhynchus mykiss Population Model

Our review of the *O. mykiss* population model is organized into the following sections that address model structure, results, and conclusions. For this review, we focused our attention on the document that we refer to as the modeling report (Stillwater Sciences 2017b).

5.1 Model structure, parameterization, key assumptions and outputs

The Tuolumne River *O. mykiss* population model is a spatially explicit (1D) model that uses an individual-based framework to represent the major life history processes affecting *O. mykiss* maturation, spawning, egg incubation, juvenile growth, movement, mortality and anadromy rates to estimate juvenile and smolt production and end-of-year age-2 and older fish (assumed to reflect adult abundance) as a function of varying flows and water temperatures in the lower Tuolumne River (Stillwater Sciences 2017b).

The model is not a full life-cycle model, as it uses a preset, specified number of resident *O. mykiss* trout to initiate the modeling process, and for some model configurations, a preset number of anadromous steelhead pre-spawners that can co-mingle with resident fish spawners. From these spawners and for a given spawning class, the model projects the number of progeny that would survive to become either smolt emigrants or resident trout that would rear to different ages. The model makes no attempt to complete the life cycle of the emigrant smolts and return them to their natal spawning grounds to begin another generation. Similarly, the model does not enable the surviving resident trout to mature and initiate subsequent generations. As a result, the model does not predict equilibrium abundance levels (i.e., average abundance over multiple generations) that would be expected to occur under a prescribed set of management actions from the initialized number of fish used to begin modeling.

As an individual-based model, the model was designed to track each fish produced from the initial spawners along the river on a daily basis, enabling the fish to grow as a function of food availability, water temperature, and population density. The model allows the fish to move in response to density adjustments, flow, and growth. Fish advance from the fry stage, to the juvenile stage, and then to different aged fish as they grow and survive. Surviving juveniles that reach certain ages can attain smolt status, depending on their parentage (i.e., anadromous fish parents or prescribed percentages of mixed parentage). Hence, the parentage of each fish is tracked in the model with respect to whether the male or female parent is a resident trout or an anadromous fish. Individual fish die as a result of prescribed mortality rates (either a background continuous rate or through an assumed predation rate if they are moving or migrating). The model selects a random group of fish to sample for size and status (due to the large number of fish that need to be tracked), and expands this to the total surviving population to estimate population metrics at given points in space and time.

The model uses a generalized multi-stage stock production approach (Baker 2009) in which starting numbers of a particular life-stage (stock) are mathematically modeled to predict how the numbers change as the cohort goes through subsequent life stages. The model incorporates both density-independent and density-dependent survival factors to reflect how both habitat quality and quantity along the river is expected to affect population performance by life stage. The model, therefore, incorporates certain conventional population dynamics concepts of both intrinsic productivity and habitat capacity used in assessing salmonid population performance (Hilborn and Walters 1992; McElhany et al. 2000) and as described in Section 2.4.

The model incorporates river flow and water temperature data for prescribed locations along the entire river on a daily basis for a given WY. A dataset with 42 WYs (1972 to 2012) containing daily flow values and water temperatures is packaged with the model for analysis.

Model parameters that determine the expected effect on the survival factors affecting individual fish are defined by discrete numbers or ranges depending on certain attributes of the individual fish being tracked in the model, such as fish size and life stage.

The model also includes random elements for some mechanisms affecting life history progression, relying on probability distributions for events such as adult upstream migration timing (i.e., the timing of the spawning run, which is a model input), individual spawner age, spawning locations, fry and juvenile movements, predation related mortality, as well as size at fry and smolt emigration. Spawning fish are distributed in a manner to use the available spawning habitat. At low spawning densities the spawners apparently exhibit little or no spatial overlap in where redds are built. Superimposition of redds can occur at high spawning densities, which in the model can act to reduce the survival of the total eggs deposited. Each stock production component in the model also makes use of temporally and spatially varying environmental conditions while determining the progression of individuals within their respective life stages and promotion into the next life stage.

The model is necessarily complex because it attempts to model both anadromous individuals as well as those that do not express anadromy. *O. mykiss* are known to exhibit the most complex life history variation of all *Oncorhynchus* species (Quinn 2018) with anadromous life histories being influenced by both genetic and environmental factors (see citations contained in Stillwater Sciences 2017b). The model developers, therefore, needed to consider the influence of many factors such as parentage, age, size, growth, and temperature in trying to project the expression of anadromous versus resident life histories (see Satterthwaite et al. 2009).

To estimate the probability of smoltification on the basis of anadromous parentage, the model allows for spawning between resident and anadromous *O. mykiss*, that is, for the resident form to cross with the anadromous form. Life history forms are referred to as ecotypes. The probability of crossing between the ecotypes in the model is determined by the relative abundance of the two types and application of data on patterns of crossings between *O. mykiss* ecotypes contained in McMillan et al. (2007); those data were used to parameterize for the probability of crossing between ecotypes. We note that McMillan et al. (2007) describes mating patterns of resident and anadromous *O. mykiss* in two rivers on the Olympic Peninsula in Washington where steelhead are abundant.

An important component of the model is how it handles movement along the river and out of the river, including the movement of fry, juveniles, other age groups and smolts. These movements affect the overall outcomes projected by the model. We draw special attention to how this is done in the model because of the near absence of information on movement by *O. mykiss* in the Tuolumne River. The modeling report is clear on this point in several places, highlighting that such information is "very limited," which is an understatement of the actual situation. As a result, the modelers made far-reaching assumptions—and simply assumed that *O. mykiss* behave in the same way as Chinook salmon fry and juveniles. Assumptions were made that *O. mykiss* fry upon emergence exhibit a substantial fry outmigration from the river like Chinook salmon fry—assuming the same percentage of fry migrants (30%) as used in the Chinook salmon model. We are unaware of fry migrations like this by *O. mykiss* fry in any rivers in the Pacific Northwest; we have extensive experience with both anadromous and resident *O. mykiss* forms using a variety of sampling methods. The life history of *O. mykiss* is very different from that of Chinook salmon, which for ocean-type Chinook salmon can produce large numbers of spawners on spawning reaches that produce large numbers of emergent fry. The fry migrant life history type of Chinook salmon is seen virtually universally in rivers that support ocean-type Chinook salmon (Healey 1991). To our knowledge, such a life history type has not been described anywhere for *O. mykiss* forms.

Similarly, movements by fry after the initial outmigration are assumed to occur in the model in the same manner as applied in the Chinook salmon model, both for fish still in the fry stage as well as juveniles after attaining that status. The relevance of these movements is that it is during movement in the model that the fish are subjected to predation by predatory fish. When not exhibiting such movement, the model applies a low mortality rate referred to as a "background rate," meant to account for losses due to disease, stranding, avian predation, and entrainment. Again, because of an absence of information on predation by fish on *O. mykiss* in the river, the modelers assumed the same mortality rates as applied to Chinook salmon during their movements. Those rates, as noted in Section 4.1.1, are based entirely on the smolt-to-smolt survival estimates derived with the RST data and they result in very high rates of loss. We concluded that those survival rates are the principal driver of the results produced by the Chinook salmon model.

It is important to recognize that the authors of the modeling report draw attention to the high uncertainty associated with the predation rates applied to *O. mykiss* in the model. Important points from page 2-4 in Attachment A in Stillwater Sciences (2017b) are the following:

- The Synthesis Study (Stillwater Sciences 2013a) suggested that aquatic predation is the primary mechanism of *O. mykiss* mortality; therefore, the *O. mykiss* model was designed to represent predation as the primary mechanism of mortality for the three relevant juvenile life stages (fry, juvenile, and smolt);
- However, predation of *O. mykiss* by predatory fish species has not been documented in the Tuolumne River; therefore, representation of juvenile mortality by fish predators in the model is based entirely on unsubstantiated assumptions;
- Stomach content sampling conducted by the Predation Study (FISHBIO, 2013a) did not identify any *O. mykiss* in predator diets; therefore, predation efficiency of fry and juvenile size *O. mykiss* for application in the model was inferred from the relative quantity of Chinook salmon juveniles observed in the gut contents of each predator type.

Besides mortality due to predation and to the other background causes listed above, the next most important source of mortality in the model is due to high water temperature. Water temperature can be a significant source of mortality in the model; the survival function associated with temperature is based on Threader and Houston (1983) and Myrick and Cech (2001).

The model can be run entirely assuming only resident *O. mykiss* are present or with a preset number of anadromous steelhead along with a preset number of resident fish. In both cases, the model starts with these preset numbers of fish that at the outset represent a number of spawners. If the starting fish numbers include steelhead, then cross mating is allowed to happen following rules mentioned above. If no steelhead are included, then the model follows the fate of the progeny produced solely from resident fish spawners. If no steelhead parents are included, smolts are still produced though at a low (assumed) rate.

The model output provides the number of surviving fish to different life stages and ages, including smolt emigrants (i.e., those exiting the river), produced from the prescribed numbers of starting fish, either resident adults alone or a mixture of resident and anadromous fish. The default initial population sizes that are preset for the model as it was delivered to us allowed for four different starting groups of spawners:

1. 500 resident fish
2. 10,000 resident fish
3. 500 resident fish together with 100 steelhead spawners
4. 10,000 resident fish together with 100 steelhead spawners.

The model documentation does not explain the rationale for using these combinations for analysis.

Recognizing that information regarding life history and production of *O. mykiss* in the Tuolumne River is limited, the model's developers state on page 4-24 of Stillwater Sciences (2017b) that the model should be used for the following:

- To examine the relative influences of various factors on in-river production of different life stages of *O. mykiss*;
- To identify critical life-stages that may represent a life-history "bottleneck";
- To compare relative changes in the population between alternative resource management scenarios.

5.1.1 RST-Based Survival Estimates and Flow-to-Survival Relationship

The *O. mykiss* population model is designed to depict the effects of alternative uses of the waters of the Tuolumne River on the productivity of native salmonid species of the lower Tuolumne River (TID/MID 2019). The response variable used is productivity, which is expressed as YOY per spawner and adult replacement rates for *O. mykiss*. There is insufficient catch of juvenile *O. mykiss* in the RSTs to support estimating survival between the RSTs. Because of this, Stillwater Sciences (2017b) used survival estimates for Chinook salmon in the *O. mykiss* population model. However, survival rates between the two species are typically different, with steelhead having higher survivals due to their larger size. Thus, steelhead-specific information is needed to inform the *O. mykiss* population model, as discussed in Section 6.3.

5.1.2 Model Structure Conclusions

Model structure and conceptual and mathematical underpinnings: It is evident that the investigators did a large amount of work in developing the model. We assume the investigators did their best to develop a useful model with the available information. We found, however, that the model's structure and conceptual underpinnings are not well supported for this species in the Tuolumne River. Because of very limited data for *O. mykiss* in the river, and particularly with regard to the possibilities for anadromy, and the obvious adaptation of the model from the Chinook salmon model including its parameterization, the *O. mykiss* model seems contrived with very questionable utility. Perhaps most confusing to us is the use of a combination of a part of the steelhead life history together with a resident population, which also does not incorporate a full life cycle—the outputs from this mixture is difficult to interpret and apply.

Model complexity: Due to the attempt to include so many facets of growth and movement in a way that might have some application to projecting both the number of smolts and surviving resident fish to different ages, we found the model to be confusing and complex. While running the model itself is easy, we found it difficult to change parameter settings and consider different scenarios than those packaged with the model.

Modeling documentation: We found the modeling report (Stillwater Sciences 2017b) to be confusing and difficult to follow given the complexity of the model. There also seemed to be a number of errors that we could not reconcile, particularly in comparing results presented in the main body of the modeling report to those presented in Attachment A of the report. Attachment A was intended to provide an update to information in the main body of the report, yet we found several inconsistencies that are difficult to understand:

- Figure 5.3-1 in Stillwater Sciences (2017b) shows results for juvenile productivity expressed as end-of-year age-0 fish per parent spawner; the values are all in the range of about 2 to 20. We could duplicate these results with the default parameter settings in the model as it was delivered to us for review in early 2020. The patterns of results in that figure shows declining productivity with declining average flow for March to September. We also note that the figure shows a pattern for density-dependence that makes sense, i.e., reduced productivity at increasing numbers of spawners. Figure 5.3.-2 shows the same productivity results for the same year class of fish in relation to water temperature (maximum 7-day average from July through September). These trends also make sense to us.
- In Attachment A, results are presented that are intended to update the results that were presented in the main body of the report. Figure 3.1-1 is intended to present an updated set of model results from those in Figure 5.3-1 of the main report. Note that the juvenile productivity values for this set of results (still for age-0 fish as in earlier figure) range from a low of about 60 to a high of about 180, much higher than the values presented in the main report. In examining the model inputs and outputs, we do not see how such values could be obtained as shown in Figure 3.1-1. Moreover, in most years the figure shows higher productivities for higher spawning escapement compared to low escapement (which is the opposite of what Figure 5.3-1 showed), yet the text states on page 3-1 that "density-dependent effects are also apparent, with consistently lower juvenile productivity predicted at the higher overall population sizes," which the figure does not show. Finally, the pattern of Figure 3.1-1 is the opposite of the pattern seen in Figure 5.3-1, where the highest productivities in Figure 3.1-1 are associated with the driest WYs—this is counterintuitive to us. The accompanying explanation (that during consistently high discharge fry and juvenile life stages are displaced to locations farther downstream into locations that may experience elevated temperatures during summer, resulting in higher mortality rates) is also the opposite of what was given in the main body of the report to explain that figure.
- An examination of Figures 5.3-1 to 5.3-4 in Stillwater Sciences (2017b) indicates that stream flows and summer temperatures affect juvenile productivity and adult replacement ratios in the Tuolumne River. That is, according to the model, wetter years generally result in higher productivities and replacement ratios, while dryer years result in lower productivities and replacement ratios. In addition, warmer summer temperatures result in lower productivities

and replacement ratios, while cooler summer temperatures result in higher productivities and replacement ratios. There is clearly an inverse relationship between flow and temperature, with flows likely driving water temperatures. This is consistent with the snorkel observations showing decreased extent of downstream habitat use by juveniles during periods of droughts that matched decreasing discharge at the La Grange gage. In general, even without the use of a model, these results make sense. On the other hand, following updates to the *O. mykiss* model (described in Attachment A of Stillwater Sciences 2017b), an examination of Figures 3.1-1 and 3.1.2 in Attachment A indicates that juvenile productivities, but not adult replacement ratios, are higher in Dry years and lower in Wet years. This is opposite of what the model predicted before it was updated. This also means that juvenile productivity is higher during warmer summers and lower in cooler summers. Interestingly, the authors did not show the relationship between summer temperatures and juvenile productivity in Attachment A like was presented in Figure 5.3-2 for the unadjusted model. The two widely contrasting results create considerable uncertainty, because the authors offered reasons for both of the two different modeling outcomes. Given these discrepancies it is difficult to embrace the *O. mykiss* model as a useful tool for evaluating the influence of various factors on the life-stage specific production of *O. mykiss* in the Tuolumne River, or for identifying life stage bottlenecks.

- These inconsistencies are difficult for us to reconcile—we can only conclude that either the modeling is in error or the documentation is incorrect—or both.

Model transparency: The model structure and progression of modeled fish through the river is not sufficiently transparent to be useful, either to interested scientists or to managers. It is not clear how the model should be used to compare results among scenarios.

Model parameterization: As noted earlier, critical parameters in the model are assumed to be the same for *O. mykiss* as they were applied to in the Chinook salmon model. For the latter, while we recognize the level of uncertainty that exists with predation rates derived from the RST-based data, the parameters in the Chinook salmon model for the most part seemed reasonable and well founded. This is not the case for the *O. mykiss* model.

Life-cycle application: Like the Chinook salmon model, the *O. mykiss* model is not a full life-cycle model. While we did examine the results of Chinook salmon in a manner to draw inferences about possible implications to the life cycle of Tuolumne Chinook salmon, a similar exercise cannot be done for the *O. mykiss* model. We find that attempting to draw conclusions about either anadromous steelhead or resident trout in the Tuolumne River based on the *O. mykiss* model would be contrived and not helpful.

Calibration and validation: The model developers attempted to calibrate the *O. mykiss* model to population estimates for resident trout made by snorkeling. This was done even though one of the years involved apparently had a very large number of immigrant trout that moved into the lower river from spill that occurred at Don Pedro and La Grange dams. An examination of Figures 5.1-1 to 5.1-4 (and Figures 2.4-5 to 2.4-7 in Attachment A) in Stillwater Sciences (2017b) compares results of modeling to snorkeling survey results. The investigators note that the model tends to underestimate the abundance of age 2-4 fish and overestimate age 1 and 5+ fish in low abundance years. In 2011, a high abundance year as estimated by snorkel survey data, the model underpredicted total population size. They also note the model underestimates the number of individuals in each age class compared to observed data. Based on this, it was concluded that, overall, the model estimates compare reasonably well with the observed data, except for 2011. It is not clear if these discrepancies are a result of issues with the snorkel data (on page 5-4 of Stillwater Sciences [2017b] the investigators suggest this is the case), an issue with the model, or both. Also, the criteria used to determine that model results compare reasonably well with observed data were not provided which hindered the interpretation of calibration results.

Perhaps of greater concern to us is whether a model like this can be calibrated and validated for its intended application—that is, to be informative with regard to implications for anadromous steelhead—when it does not appear that there are any anadromous *O. mykiss* using the river. The authors of the modeling report stated similarly on page 6-1 of their report: "In the absence of reliable information on the numbers and timing of any anadromous *O. mykiss* spawning and the factors contributing to anadromy in the Tuolumne River, the relative changes in the production of *O. mykiss* smolts resulting from different flow and temperature conditions within the Tuolumne River cannot be reliably assessed using the TROm model." We concur with that conclusion.

5.2 Modeling Results

After reviewing the various aspects of the model's structure, its conceptual and mathematical underpinnings, parameters, and assumptions, we probed the model's performance to assess patterns of outcomes. It is important to point out here that we are not entirely sure that we were provided the most up-to-date model version for our review because of certain inconsistencies that we found between our modeling results and those in Stillwater Sciences (2017b). We assume that we had the most up-to-date version but as we noted in Section 5.1.1 (second bullet under "Model documentation") we were unable to reproduce certain results that are given in Attachment A of Stillwater Sciences (2017b); that attachment is supposed to represent updated modeling results compared to those presented in the main body of that report. Despite this uncertainty, we used the version of the model that we were provided to complete this review.

Our main interest for this model was to better understand the patterns of response in the model to the primary environmental factors that appear to be of greatest concern to the species, namely flow and temperature. Therefore, we ran the model with default settings for the four preset starting populations as listed above in Section 5.1. We realized that the model, in our opinion, was not providing useful information about what could be done to benefit steelhead for the reasons stated above in Section 5.1; therefore, we focused our efforts on trying to better understand the model's outputs for resident trout in relation to flow and temperature. The authors of the modeling report apparently had the same opinion, choosing only to present findings related to environmental factors on the results for resident trout (for example, see Figures 5.3-1 to 5.3-4 in Stillwater Sciences 2017b).

We examined the same metrics that Stillwater Sciences (2017b) used in its analysis, namely what it referred to as juvenile productivity or adult productivity (the latter being called adult replacement rate in the report). These metrics, as used in the modeling report, are not equivalent to intrinsic productivity, which removes any effect of population density on survival. The *O. mykiss* productivity metrics used by Stillwater Sciences essentially correspond to the metric used to evaluate the Chinook salmon model, which in that case was expressed as emigrant smolts per female spawner. These productivity metrics represent the combination of density-independent and density-dependent survival. However, we note that the values obtained with a starting resident trout population size of 500 fish should, in effect, reflect intrinsic productivity because of the extremely low population density in that case.

Two productivity metrics are presented: 1) the number of end-of-year age-0 juveniles produced per parent spawner and 2) the total number of end-of-year age-2 and older fish (assumed to reflect adult abundance) produced per the age-2 starting population size that is pre-set in the model.

The modeling results we obtained suggest that the major driver of population performance for resident trout is water temperature. Using the water temperature metric for the maximum weekly (7-day) average temperature (MWAT) at RM 39.5, strong linear relationships are seen between MWAT and both the juvenile and adult productivity results over the 42-year data record available in the model (Figure 21). As noted above, these metrics derived with a starting population of 500 fish should reflect the direct effect of water temperature on population intrinsic productivity. We note that the slope of the regression line for age-2 and older fish is particularly steep.

Figure 22 presents patterns of response for the two population metrics to average daily flow for the months of June to August, where flow is measured at the La Grange gage. The patterns show that the productivity metrics rapidly increase from very low average flows of less than 100 cfs to a point of about 300 cfs, and then essentially stabilizes for both age groups of resident trout. Note that we were not able to understand the productivity value for 2006 for age-0 fish, highlighted as red in Figure 22. Figure 23 shows the same results but with flows up to 500 cfs shown to illustrate that the critical flow appears to be about 300 cfs. Stillwater Sciences (2017b) illustrates the effect of flow using an average flow for the months of March to September. Using that longer period of time, similar patterns are seen as in Figure 22 but, in our opinion, averaging flow over the 6-month period obscures information as to how the temperature and flow factors are working together.

Figure 21
Relationships between MWAT at RM 39.5 and estimated juvenile (top) and adult (bottom) productivity for *O. mykiss* with 500 fish starting resident population.

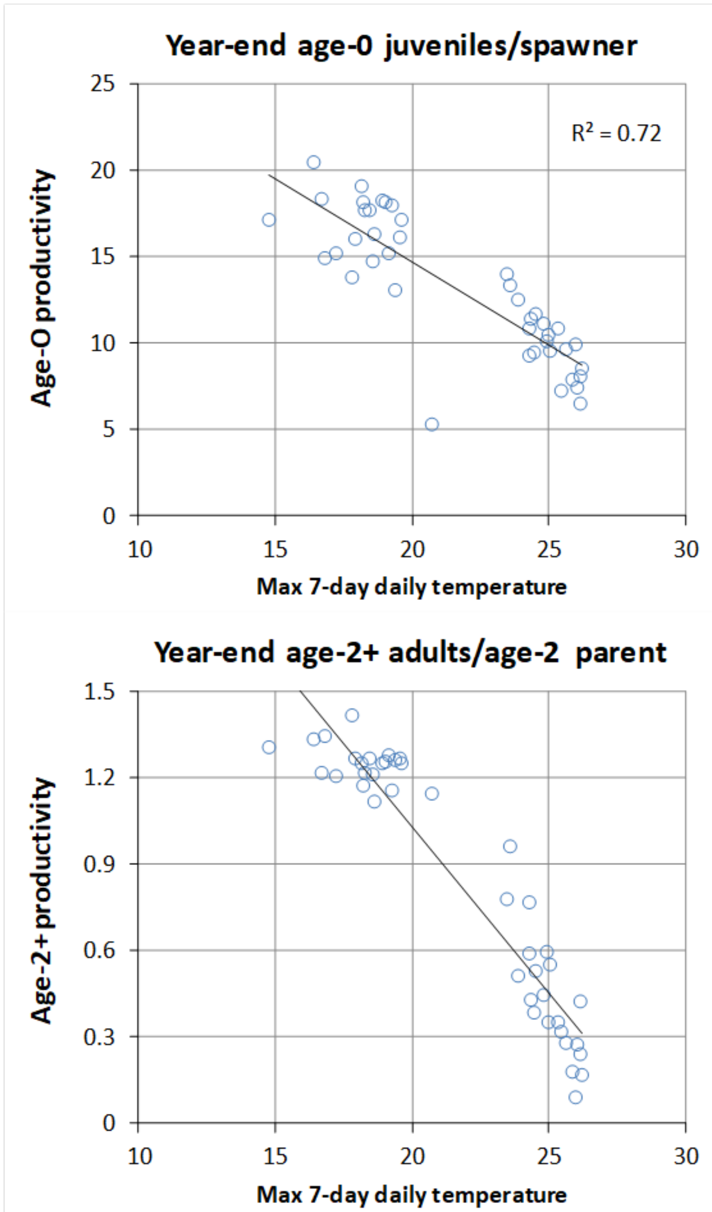
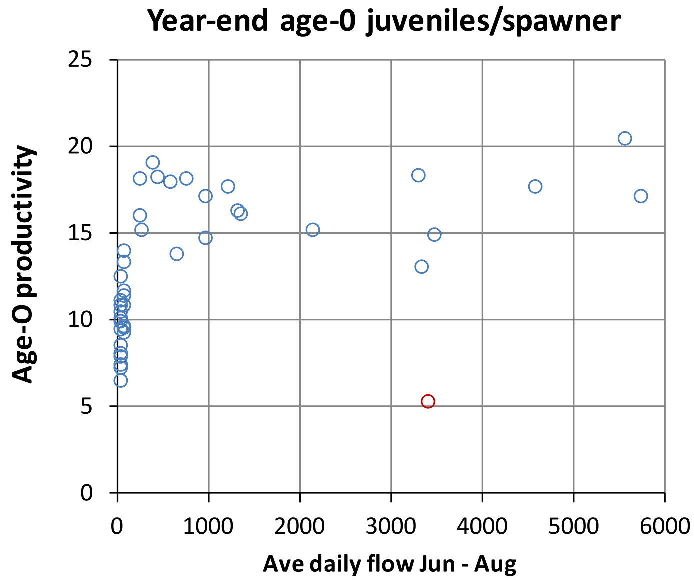


Figure 22
Plots of estimated juvenile (top) and adult (bottom) productivity for O. mykiss with 500 fish starting resident population with average daily flow at La Grange. Data point for 2006 is highlighted in red.



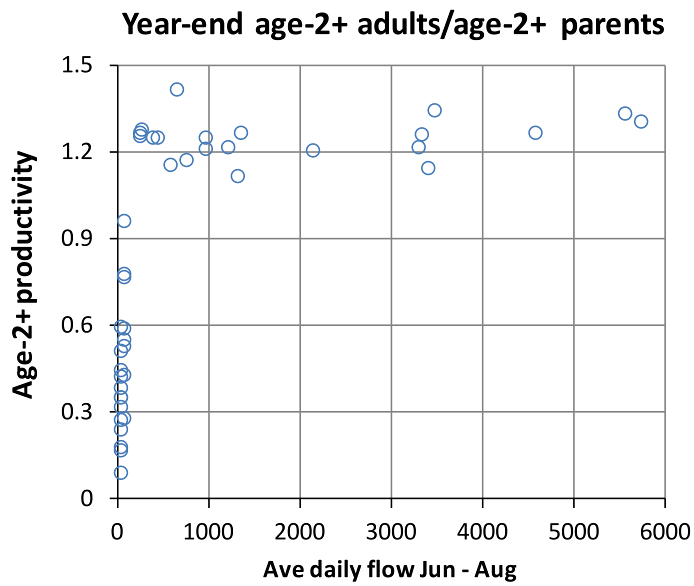
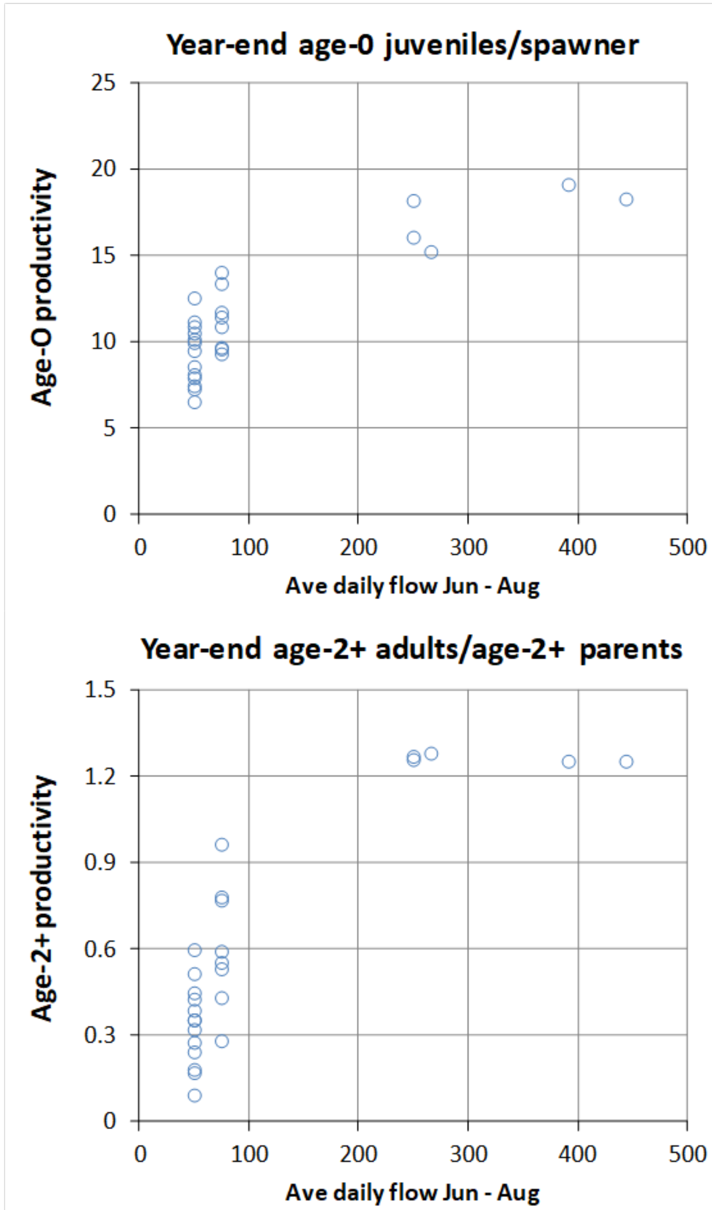
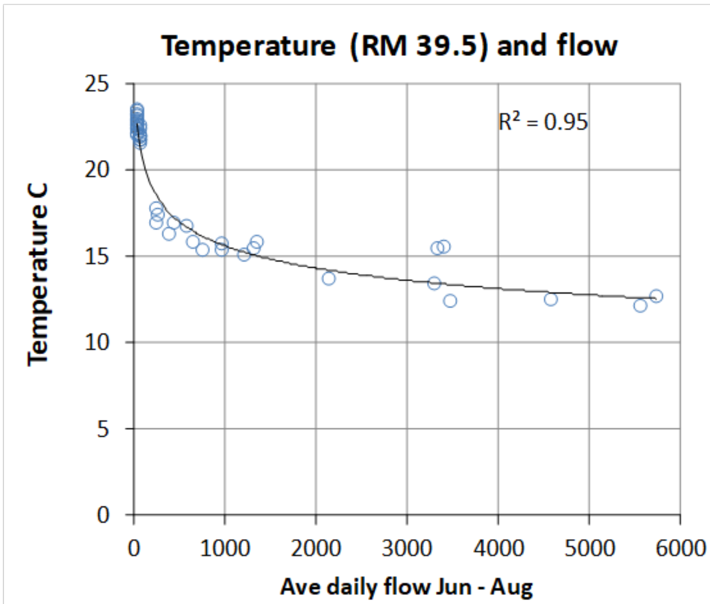


Figure 23
Plots of estimated juvenile (top) and adult (bottom) productivity for *O. mykiss* with 500 fish starting resident population with average daily flow at La Grange (with a flow axis maximum of 500 cfs).



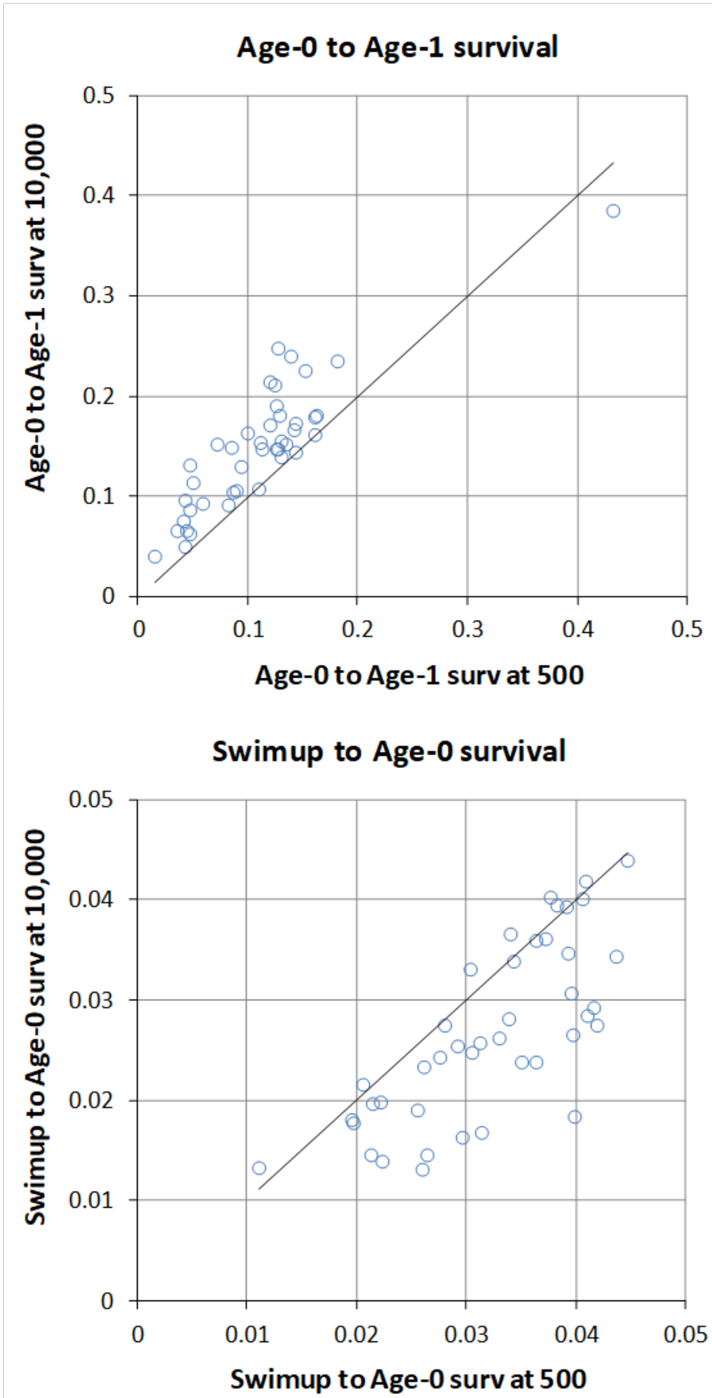
The relationship of flow and temperature during the months when temperatures are most relevant is seen in Figure 24, using the flow and temperature data packaged with the model. The amount of flow being released at La Grange Dam is clearly the major factor influencing average water temperature occurring at RM 39.5. We conclude that while water temperature appears to be the primary driver affecting the performance of *O. mykiss* in the river, the amount of flow being released at La Grange Dam is a major driver of water temperature downstream of the dam.

Figure 24
The relationship between the average daily flow released at La Grange Dam in June to August and the average daily temperature at RM 39.5 for the same months using data supplied with the O. mykiss model.



Close examination of modeling results shows some inconsistencies that we cannot explain. For example, Figure 25 (top panel) plots survivals calculated with modeling outputs for each year modeled of fish from the end-of-year at age-0 to end-of-year at age 1 for results obtained with starting populations of 500 and 10,000 resident fish. We would expect that survival would be less for the scenario with a starting population of 10,000 resident fish due to density-dependence that should be operating in the model. However, Figure 25 (top panel) shows an opposite pattern, with calculated survivals substantially higher from age-0 fish to age-1 fish with a starting population of 10,000 fish. Data points that occur above the straight line on the graph indicate that survivals calculated with a starting population of 10,000 fish are higher than values calculated for the same years with 500 fish starting populations. Plotting the same information for fish from the swim-up stage to the end-of-year for age-0 fish at 500 and 10,000 fish starting population sizes produced results that we expected and that show a strong density-dependent effect on survival in the direction it should (Figure 25, bottom panel). The pattern seen in Figure 25 (top panel) raises questions about the internal calculations being done in the model at different population densities. As noted above in Section 5.1.1, we are also concerned about inconsistencies that seem to exist in Attachment A (addendum) to the modeling report.

Figure 25
Top: Comparison of age-0 to age-1 survivals calculated with 500 and 10,000 spawners.
Bottom: Comparison of swim-up fry to age-0 fry survivals calculated with 500 and 10,000 spawners.



5.2.1 Model Limitations

The *O. mykiss* population model is being used to evaluate rearing habitat and its effects on productivity. We evaluated how the model estimates rearing habitat by reviewing assumptions and model predictions.

We identified several important issues with the *O. mykiss* model. Perhaps the greatest shortcoming of the *O. mykiss* model is the lack of *O. mykiss* data from the Tuolumne River to populate and validate the model. As a result, the model development had to rely on *O. mykiss* data from other systems or use Chinook salmon data, which is not appropriate because *O. mykiss* and Chinook salmon have different life histories and behaviors. Even the *O. mykiss* data collected within the Tuolumne River are questionable. For example, predation studies found no *O. mykiss* in predator diets. Certainly, some level of predation on *O. mykiss* seems likely in the Tuolumne River, but this was not observed or quantified. The model also relies heavily upon snorkel data and to a lesser extent on seine data. These data, without adjustments for detection efficiency, are biased and the bias varies with fish size, habitat conditions, and time of day and year. The lack of useful data not only affects model performance, but also calibration and validation of the model. In addition, the model fails to deal with recruitment of *O. mykiss* from locations outside the project area. *O. mykiss* can recruit to the project area from locations upstream from La Grange Dam. The Districts acknowledged that recruitment of *O. mykiss* from upstream locations can confound the result of the model. Recruitment from “outside” sources should have been considered in the model. This recruitment may be why according to Figures 5.1-3 and 5.1-4 (Stillwater Sciences 2017b) the model significantly underpredicted the number of fish in both size classes in 2011 relative to snorkel survey estimates. Below we expand on some of these issues.

As with the Chinook salmon model, PHABSIM modeling was used to estimate changes in *O. mykiss* fry, juvenile, and adult rearing habitat with changes in stream flows. We found no issues with the PHABSIM modeling. We appreciate the fact that fry and juvenile habitat for *O. mykiss* was quantified at flows that inundate floodplain habitat. Unfortunately, there were no efforts to quantify adult *O. mykiss* habitat at flows greater than 1,200 cfs.

Because there are virtually no data on *O. mykiss* fry and juvenile mortality and movement in the Tuolumne River, the Chinook salmon data are applied to the *O. mykiss* model. For example, the Chinook salmon emigration rate of 0.3 is applied to emergent *O. mykiss*. This means that 30% of *O. mykiss* fry leave the river following emergence. We can find no justification for this rate. Importantly, these fish, like Chinook salmon fry, do not contribute to estimated productivity (they do not reside in the river and are essentially dead in the model). In addition, the model does not allow juvenile *O. mykiss* to seek thermal refugia even though juveniles do seek thermal refugia, which Stillwater Sciences (2017b) acknowledges in Section 4.1.4.2. Overall, the lack of *O. mykiss* data to populate the model and the use of Chinook salmon data is a major shortcoming and concern with the *O. mykiss* model.

The model assumes predation is the primary agent of mortality on fry, juveniles, and smolts when they move. However, predation studies in the Tuolumne River found no evidence of predators consuming *O. mykiss* fry, juveniles, or smolts in the Tuolumne River. Instead, it was simply assumed that predation rates on Chinook salmon would also apply to *O. mykiss*, even though the predation studies do not support this assumption.

As with the Chinook salmon model, there may be an interaction the model is missing. Anytime a fish is moving (displaced or otherwise), the model applies a "migration mortality" for as long as the fry are in motion. This is intended to capture losses due to predation. However, displacement is likely correlated positively with flow, and predation is likely correlated inversely with flow. Thus, during higher flows, more fish are displaced, but they may experience lower predation rates. It is unclear if the model captures this interaction.

As noted earlier, we believe the investigators were not able to validate the model. Model calibration was carried out by comparing age structure and summer-rearing population sizes from the calibrated model to population estimates based on snorkel surveys. The comparison of modeled estimates to snorkel estimates appears problematic. Snorkeling is a useful technique for describing habitat use and distribution, but it is a less reliable technique for estimating population sizes unless the estimates are adjusted for detection probability. The probability of detecting fish during snorkel surveys is affected by many factors including fish size and age, species, habitat conditions (e.g., water clarity, depth, complexity, temperature, flow), time of day, and time of year. Unless snorkel counts are adjusted for detectability, population estimates should be considered biased. We found no information indicating that snorkel counts were adjusted for bias. Thus, we believe the attempts to calibrate and validate the model were likely based on biased data. Stillwater Sciences (2017b) acknowledges that the lack of *O. mykiss* data limits opportunities to calibrate and validate the model. We agree and believe the results from the model should be considered suspect given the issues with calibration and validation.

Section 6 of the *O. mykiss* modeling report (Stillwater Sciences 2017b) sums up our thoughts regarding the ability of the *O. mykiss* model to estimate smolt production where it states "In the absence of reliable information on the numbers and timing of any anadromous *O. mykiss* spawning and the factors contributing to anadromy in the Tuolumne River, the relative changes in the production of *O. mykiss* smolts resulting from different flow and temperature conditions within the Tuolumne River cannot be reliably assessed using the TROm model." Based on our review of the model, we would suggest the statement applies to all life stages of *O. mykiss* in the Tuolumne River. The absence of site-specific *O. mykiss* data, the reliance on Chinook salmon and out-of-basin data sources, the lack of calibration and validation data, the large number of simplifying assumptions, and biases associated with snorkel data renders the model mostly useless for evaluating the influence of various factors on the life-stage specific production of *O. mykiss* in the Tuolumne River, or for identifying life stage bottlenecks. Thus, we do not believe the *O. mykiss* model can be used to evaluate the importance of rearing habitat on *O. mykiss* productivity or replacement ratios.

5.2.2 Spawning Habitat

Stillwater Sciences (2017b) used PHABSIM modeling to quantify the amount of spawning habitat available at different flows within the river. Given our experience with PHASIM modeling, we do not fault the investigators for using PHABSIM in the population model. Unlike with the Chinook salmon model, in the case of the *O. mykiss* model, the researchers included depth curves for spawning with no upper boundary. That is, provided there are suitable velocities and substrate, *O. mykiss* can spawn within a large range of depths. This is appropriate and we believe this should have been included in the Chinook salmon model.

PHABSIM modeling results, based on modeling spawning habitat at flows from 50-1,200 cfs, suggest that spawning habitat is maximized at about 500-800 cfs among all survey reaches. It is unclear if higher flows (>1,200 cfs) would have activated additional spawning habitat along the river because the effects of flows greater than 1,200 cfs on spawning habitat were not evaluated by Stillwater Sciences (2017b).

Stillwater Sciences (2017b) reported there is no or little evidence of redd superimposition by *O. mykiss* in the Tuolumne River. Nevertheless, it was assumed to occur within the model framework. Furthermore, it was assumed that the level of egg mortality is proportional to the degree of redd overlap. In other words, if about 10% of a given redd is disturbed by a later spawning female, the egg mortality is also assumed to be 10%. The investigators provided no justification for this assumption. In our opinion, this is not a reasonable assumption and can lead to overestimation of the negative effects of redd superimposition on production. Redd superimposition can occur, but it does not necessarily result in proportional egg loss. This is because eggs are not deposited evenly throughout the area of a given redd. Instead, eggs are deposited in one or more egg pockets located within the disturbed area of the redd. Only when a later arriving female digs up an egg pocket will there be some level of mortality. A detailed study of parentage from deoxyribonucleic acid (DNA) would help inform the effects of redd superimposition on *O. mykiss* survival.

The investigators used an egg-to-fry survival of 45% for *O. mykiss*, which appears to be based on work conducted in the Tuolumne River. In contrast, they used an egg-to-fry survival of 32% for Chinook salmon. As noted earlier, it is not clear why the rate used for *O. mykiss* is considerably greater than the rate used for Chinook salmon, given that both species use essentially the same spawning areas. Gravel augmentation for *O. mykiss* is modeled by increasing the egg-to-fry survival rate from 45% under current conditions to 70% under the gravel augmentation scenario (TID/MID 2019). It is unclear why this value was chosen or if it reflects reality under a gravel augmentation scenario.

Although we found some issues with the modeling of *O. mykiss* spawning habitat, overall, we agree with Stillwater Sciences (2017b) conclusion that spawning habitat is not limiting in the Tuolumne River. Indeed, the report states that that the estimated available gravels could support an escapement of 803,000 to 855,000 *O. mykiss*.

5.2.3 Fry and Juvenile Rearing Habitat

Stillwater Sciences (2017b) used PHABSIM modeling to quantify the amount of *O. mykiss* fry and juvenile habitat available at different flows within the river. For both life stages, they quantified habitat at flows that inundate floodplain habitat. For both life stages of *O. mykiss*, suitable habitat increases substantially with flows greater than 1,000 cfs. The maximum usable fry habitat appears to occur between 4,000 and 6,000 cfs (excluding the lower two reaches). The maximum suitable area for juveniles appears to occur at flows greater than 6,000 cfs. The investigators seem to downplay the large gain in fry and juvenile habitat by noting that the 2-D model-derived estimates at the site scale may not represent all conditions occurring river wide. However, even if the lower two reaches (Riverdale Park to mouth) are removed from the analysis, there is still a large increase in usable habitat for *O. mykiss* fry and juveniles. Not only is there more usable fry and juvenile habitat at higher flows, there will be less predation on these life stages. That is, as noted in Section 2.2 of Stillwater Sciences (2017b), predation risk decreases with flows as floodplain inundation occurs and predators feed more effectively in-channel than on inundated floodplains and along banks.

Reach-specific estimates of carrying capacity were calculated for O. mykiss fry and juveniles. It appears WUA data were used for fry and juveniles to calculate habitat capacity. However, WUA data for flows less than 1,200 cfs were referenced and it is not clear if the model allows carrying capacity to vary with stream flows. To evaluate the effects of floodplain inundation (flows greater than 1,200 cfs) on fry and juvenile capacity, changes in capacity with changes in WUA at flows greater than 1,200 cfs would need to be evaluated. It is not clear if this was done. This is important because it affects fry and juvenile movement and mortality in the model.

5.2.4 Water Temperature

Rearing *O. mykiss* in the lower Tuolumne River are subjected to elevated water temperatures along the majority of the river downstream of La Grange Dam in most years. The model, as provided to us along with relevant flow and temperature data packaged with the model, clearly demonstrates strong relationships between juvenile and adult *O. mykiss* productivity and water temperatures, both in relation to average summer temperatures and MWAT in the lower Tuolumne River. As shown in Figure 24, water temperature and flows are correlated in the lower river, most notably during summer when *O. mykiss* are rearing. The correlation is not surprising. As seen in Figure 23, productivity reaches an asymptote with flow at around 300 cfs; our analysis also shows that the total numbers of year-end age-0 and age-1 rearing fish achieve maximums at about this same flow level, suggesting that the capacity for young fish is being reached. We conclude from these patterns that intrinsic productivity of *O. mykiss* is primarily being driven by water temperatures in the river. As discussed in Section 2.4 of this report, intrinsic productivity is likely the most important characteristic of viability for *O. mykiss* under prevailing conditions and for conditions expected with climate change. Therefore, based on the *O. mykiss* population model, we conclude that water temperature has a significant effect on *O. mykiss* productivity within the Tuolumne River.

5.2.5 Stimulating O. mykiss Anadromy

Extensive habitat loss has resulted in the threatened status of *O. mykiss* in California's Central Valley, and given this, populations in dam tailwaters in the San Joaquin River basin are important for conservation because they could be the only representatives of a presumably ecologically distinct segment of the ESU (Lindley et al. 2006). However, water releases from dams change the thermal regime and food web structure of the river downstream from the dams (Lieberman et al. 2001, as cited in Lindley et al. 2006) in ways that may provide fitness advantages to resident forms of *O. mykiss*. Indeed, observations in the Sacramento River below Shasta Dam, Stanislaus River below Goodwin Dam, and Clear Creek below Whiskeytown Dam indicate that large areas of stable habitat in dam tailraces may promote the residualism of anadromous trout (Reclamation 2008).

This appears to be the case in the Tuolumne River, because observations of both age 0+ and older age classes of *O. mykiss* during snorkel surveys occurred at locations upstream of the Roberts Ferry Bridge (RM 39.5) (Stillwater Sciences 2013a) and steelhead abundance is low. A total of approximately 21 adult O. mykiss were counted at the weir located at RM 24.5 from 2009 through May 2013 when river flow less than 1,400 cfs supported weir operation, although fish not counted could have immigrated under higher flows (Stillwater Sciences 2017b). From fall 2013 through December 2019, a total of 4 adult *O. mykiss* were counted at the weir (reported in annual reports submitted to FERC [e.g., TID/MID 2020a]). Zimmerman et al. (2009) analyzed otolith strontium:calcium ratios to determine the maternal origin and migratory history of rainbow trout collected in Central Valley rivers. They concluded that *O. mykiss* sampled from the Tuolumne River were dominated by rainbow trout progeny, not steelhead progeny, and five of 964 fish sampled from all Central Valley locations were confirmed to be adult steelhead, with one of the five being from the Tuolumne. These findings comport with Stillwater Sciences (2017b), which indicated that little information was identified to suggest there is a self-sustaining steelhead population on the Tuolumne River. Zimmerman et al. (2009) also reported that steelhead progeny were present at all Central Valley sites sampled, which suggests the genetic material needed to express anadromy is present in the Tuolumne River.

Lindley et al. (2007) state that even though there are different forms of *O. mykiss*, the steelhead form is important to the viability and long-term persistence of the species and is critical to the conservation of the population (Travis et al. 2004; Bilby et al. 2005 as cited in Lindley et al. 2007). The

Tuolumne River *O. mykiss* population model should inform how operations and management scenarios stipulated in the license will affect the expression of anadromy over the license period including under future climate conditions. This is based on the role steelhead have in the viability and recovery of the DPS listed under the ESA, which includes naturally spawned steelhead originating below natural and manmade impassable barriers from the Sacramento and San Joaquin rivers and their tributaries but does not include resident rainbow trout.

Section 6 of Stillwater Sciences (2017b) states "the relative changes in the production of *O. mykiss* smolts resulting from different flow and temperature conditions within the Tuolumne River cannot be reliably assessed using the TROm model" and concludes the model is limited to evaluation of the suitability of specific river reaches for any smolt-ready individuals within the overall anadromous-resident population with respect to temperature. Given the assumption of a fixed and very low rate of anadromy from resident parents (on the order of 2%; Section 4.2.5; Stillwater Sciences 2017b), this suggests the expression of anadromy in the current model is constrained. Stillwater Sciences (2017b) addresses the topic of anadromy and clearly recognizes its importance in a modeling framework for *O. mykiss*. Tools for incorporating this life history component into the analytical framework are available. Satterthwaite et al. (2010) developed a modeling framework to predict evolutionary endpoints for the steelhead life history in response to management actions that change stage-specific survival or growth rates. Their evolutionary optimization models successfully predicted the life history displayed downstream from dams in the American River (all anadromous with young smolts) and Mokelumne River (a mix of anadromy and residency).

Stillwater Sciences (2017b) discusses Satterthwaite et al. (2010) and points out that the populations modeled were not observed or predicted to exhibit a predominantly resident life history like the Tuolumne River *O. mykiss* population and "thus the applicability of the Satterthwaite et al. (2010) approach to determining the probability of smolting among Tuolumne River *O. mykiss* is uncertain." Uncertain is not the same as undoable. Satterthwaite et al. (2010) model growth as a function of environmental conditions and use sensitivity analyses to predict likely evolutionary endpoints under changed environments. The approach used follows the state dependent life history model of female steelhead described in Satterthwaite et al. (2009), and where parameterization is based on site-specific growth, survival, and fecundity data. In the Tuolumne River *O. mykiss* model, juvenile growth for fry and parr are represented by Equation 4, which is based the growth model presented in Satterthwaite et al. (2009). Therefore, it appears to us that the information needed to undertake analyses similar to those conducted in the American and Mokelumne rivers and incorporating the expression of anadromy more explicitly in the Tuolumne River *O. mykiss* modeling framework is available. Given the need to focus management actions on steelhead, this warrants further discussion.

We understand that the *O. mykiss* population model was constructed to address within-river population dynamics. We believe that limiting modeling to only the life stages within the river using pre-set model parameters for how anadromy is expressed does not provide the type of information resource managers need to understand how water project operations can be used to stimulate the expression of anadromy. That is why we recommend incorporating a different modeling framework into the *O. mykiss* model to predict likely evolutionary endpoints under changed environmental conditions (see Section 6.8).

5.2.6 High Priority Assigned to Predation

The comments presented in Section 4.2.6 on Chinook salmon apply to the *O. mykiss* model regarding changes in smolt survival because it uses the same flow-to-survival relationship as is in the Chinook salmon model. However, this is a moot point because based on the empirical information, the number of *O. mykiss* smolts produced in the Tuolumne River is extremely low in some years and zero in many years.

5.3 Model Conclusions

In contrast to the Chinook salmon population model, we found that the *O. mykiss* population model is poorly designed to be used for diagnosing or evaluating management actions related to the anadromous form of this species, given the model's current structure, its parameterization, and its calibration and validation. The model suffers from a number of shortcomings.

The model attempts to combine an artificial and unrealistic number of steelhead spawners with two different levels of resident fish spawners in a manner that appears contrived, not transparent, and difficult to follow in both the model and the model documentation. The conceptual underpinnings of doing this in the model are not well supported. We found several inconsistencies between the original and updated modeling results that remain unresolved, which raised further concerns to us about the reliability of the model.

Foremost among its problems, the model is structured and parameterized based on concepts and parameter settings used in the Chinook salmon model. The life histories of these two species are dramatically different. A model structured to accommodate juvenile Chinook salmon is inappropriate to address the needs for *O. mykiss* modeling, especially for the anadromous form. Movement patterns of fry and juveniles of ocean-type Chinook salmon are much different than those of juvenile *O. mykiss*, whether in the anadromous or resident form (Quinn 2018). Models developed to assess responses of these two species to freshwater environmental factors, therefore, need to account for the differences in life history patterns between the species in how each individual model is structured and parameterized (Blair et al. 2009).

A key assumption in the *O. mykiss* model is that predation by predatory fishes is a major cause of poor performance *O. mykiss*, and presumably to the production of the anadromous form of the species. Three parameters within the model were parameterized based on the results of the RST data as it was used to estimate smolt-to-smolt survival of Chinook salmon. However, there is no evidence that predation on *O. mykiss* is comparable to or similar in any way to that of juvenile Chinook salmon. In fact, there is no evidence of predation on juvenile *O. mykiss* by predatory fishes in the Tuolumne River (Stillwater Sciences 2017b, page 2-4 in Attachment A).

Another major shortcoming of the model is an inability to be adequately calibrated or validated, due to limited amounts of information available for *O. mykiss* in the river. The authors of the *O. mykiss* modeling report recognized this limitation. They stated: "In the absence of reliable information on the numbers and timing of any anadromous *O. mykiss* spawning and the factors contributing to anadromy in the Tuolumne River, the relative changes in the production of *O. mykiss* smolts resulting from different flow and temperature conditions within the Tuolumne River cannot be reliably assessed using the TROm model." We agree with this assessment.

We found that the factors affecting anadromy of *O. mykiss* in the Tuolumne River were not adequately addressed. It would be more useful to apply a framework like the one described by Satterthwaite et al. (2009, 2010) to *O. mykiss* in the Tuolumne River to examine potential anadromy, rather than to apply the model reviewed that focuses on resident trout.

Despite these shortcomings, it bears noting that the model, as developed, found water temperatures to be the major environmental factor driving juvenile *O. mykiss* productivity downstream of the dam. Flows released below La Grange Dam are apparently the major factor affecting water temperatures.

6 Recommendations

We concluded that the Chinook salmon population model is useful but not usable by all stakeholders and the *O. mykiss* population model is neither useful nor usable. From our perspective, solutions exist for the issues we raised with the models. Therefore, we organized our thoughts on how to resolve the issues into eight overarching recommendations. For the Chinook salmon population model, the recommendations address increasing confidence with its parameterization and characterizing the scientific uncertainty associated with results (Sections 6.3, 6.4, and 6.7). The recommendations address key aspects of managing the river over the term of the FERC license that are missing from the current analytical framework (Sections 6.1, 6.2, and 6.6) and the need for additional information to improve the model and better inform management decisions that are based on the model (Sections 6.3, 6.5, and 6.7). To identify solutions to the issues we see with the *O. mykiss* population model, we provide a suggested path forward in Section 6.8. In addition, the need to establish performance goals (Section 6.1) and incorporate climate changes into the analytical framework (Section 6.2) apply to the *O. mykiss* population model as well as the Chinook salmon population model. Implementing these recommendations will improve the understanding of key relationships between the species modeled and their environment and analyses of alternatives designed to improve salmonid productivity in the lower Tuolumne River.

6.1 Establish Population Performance Goals for Both Species

Based on TID/MID (2019), the population models have been used to assess individual river management alternatives for each species. In other words, alternative "X" will produce "Y" for Chinook salmon or *O. mykiss*. We did not find any discussion or sensitivity analysis of what would be required to achieve specific production or productivity goals or targets. Each species is addressed separately and there was no apparent discussion of how to optimize management alternatives for both species at the same time or identify tradeoffs between species and alternatives that would have to be discussed. A key attribute of quantitative models is that they support these types of analyses and discussions.

6.2 Incorporate the Effects of Climate Change into the Analytical Framework for Both Models

Changes in precipitation patterns, water temperature, and river hydrology can affect many aspects of salmonid biology (Crozier et al. 2008a) and freshwater habitat (Beechie et al. 2012). Herbold et al. (2018) point out that limited diversity and habitat loss has already left California salmon with a reduced capacity to cope with a variable and changing climate, and that increasing temperatures and decreasing snowpack have produced harsher conditions for California's salmon in their current habitats than they experienced historically.

We did not find a discussion of how climate change is to be modeled in the documents reviewed or an analysis of the sensitivity of alternatives modeled in TID/MID (2019) to climate change. Perhaps this is the result of specific guidance from FERC, or because climate change is being incorporated into an adaptive management plan that is beyond the scope of this review. Regardless, we expected climate change would have been addressed in the Salmonid Population Information Integration and Synthesis Study Report (Stillwater Sciences 2013a) given its potential implications on salmon and steelhead. The lack of climate change in the modeling framework renders it impossible to judge how operations and actions stipulated in the license will be affected by climate, the effects this may have on salmonid population productivity, and the level of flexibility in operations available to address any impacts. Assessing the effects of drought and extended periods of drought may be especially important in regulated rivers in California (e.g., Israel et al. 2015).

Crozier et al. (2008b) found for Chinook salmon that population models can incorporate climate change predictions and that global warming poses a direct threat to freshwater stages by increasing their risk of extinction. Thus, the analytical capability exists to model climate effects, and this is now being applied to habitat restoration actions and to regulated rivers. For example, climate change was incorporated into an analysis of benefits to Chinook salmon and steelhead from habitat restoration in a large river in southwestern Washington. The results showed the level of restoration required to overcome climate change (https://chehalisbasinstrategy.com/asrp/asrp-phase-i-draft-plan/). This river is not regulated but a flood retention structure is being considered, for which the effects of increased flow magnitude and frequency associated with climate change on project operations was also evaluated (https://chehalisbasinstrategy.com/eis/sepa-process/).

There are three aspects of potential climate change to consider when managing a river over the term of a FERC license. First, climate change is projected to affect water temperature and precipitation patterns, which will affect water quality and river hydrology. Second, changes in water quality, timing, and quantity can affect salmonid biology and phenology as well as population productivity through effects on freshwater habitat. Zabel et al. (2006) found that effects associated with freshwater recruitment was consistently the most important parameter evaluated in their model and interpreted this to mean that increasing juvenile carrying capacity is needed to recover the Chinook salmon populations they analyzed. Lastly, resilience to climate change needs to be factored into habitat restoration project designs to ensure the projects are effective over the long term (Beechie et al. 2012). Each aspect of potential climate change applies to both regulated and non-regulated rivers to some degree.

Water temperature in the Sacramento and San Joaquin rivers is projected to be affected by increasing air temperature and decreased snowmelt runoff, which reduces the amount of cold water available in the upstream reservoirs to manage downstream temperature (Cloern et al. 2011). Projected increases in air temperature continue trends already observed, and central estimates of projected increases range from approximately 2.8°C (5°F) to 3.9°C (7°F) depending on location (Reclamation 2016a). For the Sacramento-San Joaquin Basin, mean annual temperature projections show an increasing trend over time (Reclamation 2016a).

The NorWeST webpage (https://www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html) hosts stream temperature data and climate scenarios for streams and rivers across the western United States. In the Tuolumne River under the A1B Greenhouse Gas Emissions Scenario, a review of changes in summer stream temperatures from historical conditions into the future in 2040 and 2080 shows the proportion of reaches upstream of Waterford above 16°F (from 16°F to 30°F) increasing through time, indicating that habitat conditions for salmonids will change during the period.

The amount of precipitation projected to fall as snow in the Sierra Nevada mountains is likely to decrease. Knowles and Cayan (2002) (as cited in PRBO Conservation Science 2011) projected that April snowpack will decline throughout the century and by 43% in the southern Sierra Nevada by 2090, and snowpack loss would be greatest at mid-to-lower elevations. Runoff will increase during fall and winter months. Peak runoff may shift by more than a month earlier in some watersheds. Spring runoff will decrease due to reduced winter snowpack. Earlier runoff will refill reservoirs earlier, which may force earlier discharge due to the flood rule curves in effect for each reservoir.

Information is readily available in the scientific literature on how to incorporate climate change into habitat restoration designs. For example, Beechie et al. (2012) found that restoring floodplain connectivity and stream flow regimes and re-aggrading incised channels are more likely to ameliorate stream flow and temperature changes and increase habitat diversity and population resilience than instream rehabilitation actions. Timpane-Padgham et al. (2017) reviewed concepts and attributes from the resilience literature to understand how to improve restoration efforts under changing climate conditions.

It has become a common practice to analyze potential climate change impacts on operations, flows, temperature, and the environment for projects like the Don Pedro Project. For example, an operations model accounting for climate change in the Tuolumne River was prepared by Kiparsky et al. (2014). Similarly, the models employed by the Districts for operations and temperature prediction have the capability to be used to analyze climate change impacts.

Therefore, climate change should be incorporated into the modeling framework to fully understand effects of river management strategies on Chinook salmon and steelhead given that FERC licenses are in place for decades, and the projected changes in temperature and snowpack noted above and their potential effects on salmonid biology, habitat, and restoration effectiveness. For example, additional model runs could be conducted using synthetic hydrological conditions that forecast effects of climatology and project operations on environmental conditions in the lower Tuolumne

River. This would inform how the productivity of Chinook salmon would be affected and whether additional management actions would be required to address the effects.

6.3 Conduct Additional Analysis of Flow Effects on Both Species

While many mark-recapture trails have been completed in the Tuolumne River, the analysis of the data beyond developing annual estimates of catch appears limited to Robichaud and English (2017), which updated a similar analysis conducted in 2012. Their analysis provides an important contribution, but additional analysis is warranted in our view. This is because of the influence survival between the RSTs has on model outputs (smolt-to-smolt survival) and the potential for catchability at each trap, and thus survival between the RSTs, to vary with environmental conditions and life stage (see Section 4.1.1).

As discussed in Section 4.1.1, Robichaud and English (2017) excluded seven data periods in 2007, 2009, 2010, and 2011 from their analysis that represented ascending flow conditions. Such periods stimulate juvenile salmon movement and the influence and sensitivity of RST catch with ascending flow periods included in the analysis should be assessed. Also, the factors affecting RST catch (e.g., flow, capture efficiency, life stage, true survival between the RSTs, rearing, and behavior) need to be addressed in an analytical framework to understand their influence on estimated survival. Additional analyses of Tuolumne River data are needed to investigate factors associated with trap efficiency, variability across years, and mark-recapture releases to develop best-fit models for each trap and life stage that address all WY types and also data dispersion. In addition, sensitivity runs using the multivariate quasibinomial GLM-based relationship between smolt survival and flow should be conducted to understand how Chinook salmon model outputs vary with the relationship selected for the population model and the influence of one data point with very high abundance and survival on model fit.

Estimated survival between the RTSs should be independently verified using telemetry methodologies. The studies should be conducted over a range of flow and environmental conditions both within years and among WY types, and estimated survival should be partitioned among the various reaches of the lower Tuolumne River. Results of the studies are needed to help inform model structure and parameterization by improving estimates of the number of smolts arriving at the Waterford RST.

FISHBIO (2013a) conducted predator abundance and diet studies in 2012 and based on these concluded that virtually all juvenile salmon migrating between the Waterford and Grayson RSTs in 2012 were likely consumed by predators. WY 2012 was characterized by generally low flow with a major peak occurring in early May and a minor peak in late May, both of short duration (Figure 1, Robichaud and English 2017).

FISHBIO (2013a) also estimated the survival of hatchery-origin Chinook salmon smolts using acoustic telemetry methodologies. Survival was not estimated using a mark-recapture model but instead was inferred based on reported detection histories at specific receiver locations, or what they termed fate determinations. The acoustic telemetry study in 2012 used appropriate techniques, the sample size was adequate (n = 222), and fish size (average fork length of approximately 108 mm) seemed appropriate. Releases were made from Hickman Bridge (RM 31.6) during three time periods in May 2012 under different flow and environmental conditions. In the first release on May 9 to 10, 2012, 37 of 75 fish were detected at the Grayson RST, which is a substantially different picture of apparent survival based on the estimated predation rate discussed above. Target flow for the release was 2,100 cfs and water temperature at Roberts Ferry was 12.6°C. Results of the last two releases in May were similar to the estimate of high loss between Waterford and Grayson discussed above. In the second release on May 16 to 17, 2012, one of 74 fish released was detected at the Grayson RST. Target flow for the release was 280 cfs and water temperature at Roberts Ferry was 16.3°C. In the last release on May 21 to 22, 2012, zero of 73 fish released were detected at the Grayson RST. Target flow for the release was 415 cfs and water temperature at Roberts Ferry was 16.7°C (Table 5.4-2, FISHBIO 2013a). This suggests to us that there are confounding effects of flow, date, and temperature in the dataset based on large differences in the fate determinations associated with releases conducted under different environmental conditions but only days apart. In addition, in 2012 a total of 600 coded wire tagged Chinook salmon were marked and released to accompany the acoustic tagged fish, but detections of these fish and trends in survival relative to the RST data, acoustically tagged fish, and estimates of overall loss to predators were not provided.

The 2012 study was a good initial step toward developing an understanding of flow-survival relationships in the Tuolumne River based on active telemetry techniques, but as a single study it informs little. FISHBIO (2013a) states that an additional year of predator abundance and predation rate sampling was planned for 2014 to expand and improve upon the knowledge gained by the 2012 study. Changes from the 2012 study plan were to include use of a robust mark-recapture design to estimate predator abundance, conducting concurrent predation rate and predator abundance sampling throughout the juvenile Chinook salmon outmigration period, and use of acoustic telemetry to identify potential mortality hot-spots. It is our understanding that the additional studies were not conducted. We concur with the need for these additional studies. The studies should be conducted over multiple years and all major flow conditions (WY types), and within each year to develop an understanding of how survival varies with multiple environmental factors. In addition, estimating survival based on mark-recapture models is needed to incorporate estimated detection probability into the survival estimates (e.g., Buchanan et al. 2013).

Acoustic tags and detection equipment continue to be updated and tag sizes reduced, and tags are readily available for use in smolt-sized fish for both Chinook salmon and steelhead the Tuolumne River. Vendors are producing tags with dimensions of 10.7 by 5.0 by 2.8 mm that weigh 0.3 gram or less, and have a tag life of 37 days with 5-second pulse repetition rates (e.g., Advance Telemetry Systems [ATS] Model SS300; Lotek L- AMT-1.416; and Vemco V3). The ATS Model SS400 acoustic tag weighs 0.222 gram, and with a 3-second pulse rate has nominal battery life of approximately 45 days. As with any telemetry study and as was addressed in FISHBIO (2013a), effects of tagging on fish behavior and survival needs to be considered, especially if the study involves large distances (Wargo Rub et al. 2020).

In addition to active tag technologies, survival can also be estimated based on passive integrated transponder (PIT) tags and the installation of instream detectors. Connolly et al. (2008) reported detection efficiencies exceeding 96% during high-flow periods and approaching 100% during low-flow periods using experimental detection arrays in two small streams in Washington. Since this initial research, the number of instream PIT tag arrays has expanded greatly as researchers seek to monitor juvenile and adult movements and understand life history patterns, including the installation of numerous arrays in large river systems (http://www.cbr.washington.edu/dart/query/pit_basin). Survival estimation methodologies based on PIT-tag detections have been available since the late 1990s (Skalski et al. 1998). Vendors continue to engineer smaller PIT tags and it is our experience that tagging now occurs in fish as small as 60 mm in the Columbia River basin, which would allow behavior and survival in smaller fish in the Tuolumne River to be evaluated.

6.4 Characterize Chinook Salmon Model Sensitivity to Data Variability

Characterizing the variability in modeled relationships is critical for understanding the sensitivity of outputs to key relationships incorporated into a model. Outputs from the Chinook salmon population model are expressed as smolts per female (Table 2.3-2, TID/MID 2019) out to two decimal places with no confidence intervals provided. This implies a false sense of precision associated with the outputs. It would be informative to understand whether the model outputs are different by viewing overlapping ranges. We understand that model sensitivity to factors potentially affecting production are presented in Section 5.2 of each report. Here we are referring to the sensitivity of the model outputs to key relationships that were characterized by variability in the data used to develop the relationships. The following seem highly influential based on our review and warrant analyses to characterize model sensitivity due to data variability:

- Figure 10 of Robichaud and English (2017) displays three relationships of survival between the Waterford and Grayson RSTs versus flow based on trap efficiency trials. While the variability in survival associated with each trail is generally low (Table 3, Robichaud and English 2017), the spread in point estimates at certain flows is extremely large. Based on a visual interpretation of Figure 10 (Robichaud and English 2017), survival around 3,000 cfs among trials ranged from approximately 0% to 50%, and around 1,000 cfs it ranged from approximately 4% to 30%. Establishing confidence intervals (or precision intervals) around the selected relationship is needed given this variability.

- The fitted intercept of survival at zero flow for the Chinook Salmon Population Model (Equation 8; Stillwater Sciences 2017a) is 0.03287, but survival should be zero at zero flow and the regressions should be recalculated and forced through the intercept. This will result is a slightly steeper flow-to-survival relationship. The Chinook salmon model could then be rerun for each alternative using the new curve and confidence intervals to view trends and overlaps in the data.
- The best-fit model identified by Robichaud and English (2017) was the multivariate quasibinomial GLM, which had an approximate R^2 of 0.41. It would be instructive to understand the influence of selecting a linear regression over the quasibinomial GLM by running the Chinook salmon model using both relationships, including confidence intervals.
- Model fit of the multivariate quasibinomial GLM was highly sensitive to one data point with very high abundance and very high survival (2011; Robichaud and English 2017). The basis for removing the influential data point and accepting a much-reduced approximate R^2 for the multivariate quasibinomial GLM was not clearly stated, and the sensitivity of modeled outputs to the inclusion or exclusion of the data point was not provided but is needed.
- Figure 2 of Robichaud and English (2017) presents fry and smolt catchability as a function of the percent flow sampled at the Waterford and Grayson RSTs. Variability in catchability of both life stages appears to increase with percent flow sampled, especially for fry at Waterford and smolts at Grayson. This indicates increased variability in catch as river flow decreases and the percent of river flow sampled in the trap increases. Because low flow is common in this river one would expect this variability to occur frequently. Calculating confidence intervals around the catchability relationships and rerunning the model such that the observed variability is included would inform the sensitivity of model results to this variability and the potential need for additional studies of trapping efficiency under lower flow conditions.

6.5 Expand Chinook Salmon Otolith Analysis

The type of information provided in Appendix A of Stillwater Sciences (2016) needs to be repeated for otoliths collected during carcass sampling conducted to date and into the future. Otoliths have been sampled consistently since 2005 and intermittently back as far as 1994.[7] Results of the analysis would produce a valuable long-term database that could be used to inform trends in natal origin, juvenile growth and residency, and the relative contributions of juvenile Chinook salmon emigrating from the Tuolumne River as fry, parr, and smolts to spawner escapement, similar to Sturrock et al. (2015). The size and age of juveniles upon exiting the Tuolumne River based on otoliths could be used to corroborate RST-based estimates and judge the utility of relying on RST-based production estimates in the Chinook salmon modeling framework. The information could also be used to

[7] Personal communication, Gretchen Murphy, CDFW, to John Ferguson, Anchor QEA, April 15, 2020.

reconstruct the in-river conditions conducive to adult escapement to help inform water management alternatives.

We note that Mesick and Marsten (2007) made a similar recommendation and pointed out the analysis should begin with a cohort of adults that reared during wet conditions when outmigrating fry would be expected to contribute to adult recruitment.

6.6 Evaluate Effects of Chinook Salmon Hatchery Strays

A growing body of literature demonstrates that hatchery fish have heritably lower reproductive success than wild fish and can reduce the fitness (productivity) of an entire population. Christi et al. (2014) combined 51 relative reproductive success estimates from six studies on four salmon species and concluded that hatchery fish averaged only half the reproductive success of their wild-origin counterparts when spawning in the wild. Here, relative reproductive success is defined as the reproductive success of hatchery-origin fish (i.e., fish whose parents spawned in a hatchery) relative to wild-origin fish (i.e., fish whose parents spawned in the wild) when both groups are allowed to spawn in the wild. Christie et al. (2014) reported that the weighted geometric mean relative reproductive success equaled 0.45 to 0.63 for hatchery Chinook salmon and 0.38 to 0.74 for hatchery steelhead. Importantly, the researchers stated, "the reduced fitness of hatchery fish was consistently documented despite differences in geographic location, study species, hatchery practices, and analytical approaches." Thus, the reduced relative reproductive success of hatchery fish is likely a general phenomenon.

A large percentage of the adult Chinook salmon that spawn within the Tuolumne River consist of hatchery and wild strays. In Appendix A of Stillwater Sciences (2016), Drs. Sturrock and Johnson reported that considering all five outmigration years combined (n = 598), 54% of the unmarked fish samples were identified as wild and of Tuolumne River origin (n = 321), 43% were identified as hatchery-origin (n = 255), and 4% were identified as wild strays from other rivers (n = 22) for fish emigrating from the Tuolumne River in the spring of 1998, 1999, 2000, 2003, and 2009. Stillwater Sciences (2016) reported that estimated total hatchery contribution to annual escapement for spawner years corresponding to the five outmigration years included in the otolith study averaged 67%. The proportion ranged from 39% to 100% and averaged 82% in the last three years evaluated, suggesting an increasing trend in hatchery-origin proportion (Table 6.1-1; Stillwater Sciences 2016). Given the large and increasing number of hatchery strays spawning in the Tuolumne River, and their effects on population fitness, the productivity of the Chinook salmon population is expected to be low and will likely decrease over time with increasing hatchery fish straying into the Tuolumne River. Mesick et al. (2008) reported that the number of adult Tuolumne River fall-run Chinook salmon produced at a given spring flow has significantly declined by about 50% in the 1997 to 2004 period compared to the 1980 to 1990 period. Mesick (2009) acknowledged this potential effect of hatchery strays on overall population productivity and states that although there are no data to show that productivity rate was directly affected by a loss of genetic viability, the likelihood that the Tuolumne River population was heavily repopulated with hatchery fish strongly suggests a causal link between genetic viability and population productivity.

Based on our review, the Chinook salmon population model does not account for potential effects of increasing straying on productivity other than accounting for less fecundity if hatchery fish are smaller (Table 4.2-1; Stillwater Sciences 2017a). The role of hatchery strays on the intrinsic productivity of wild Chinook salmon in the Tuolumne River is not well understood but needs to be factored into any modeling framework. This is because of the role flow has on habitat capacity, growth, life history expression, and size at emigration, as discussed in Stillwater Sciences (2016), and given the increasing trend in the proportion of hatchery-origin fish and the potential effects on productivity over the duration of a FERC license.

6.7 Conduct Parentage Studies to Establish Chinook Salmon Redd Superimposition Rates

Assumptions regarding redd superimposition were made in both the Chinook salmon and *O.* mykiss population models. A better approach would be to conduct a detailed study of parentage from DNA to inform the effects of redd superimposition on Chinook salmon and *O. mykiss* egg-to-fry survival.

6.8 O. mykiss Model

Based on our review of the *O. mykiss* model, we believe the next step at this point should be to focus on understanding how to stimulate anadromy and what that implies in terms of water management and project operations. With that information in hand, implications and tradeoffs between fisheries and water management goals for Chinook salmon and steelhead recovery goals can be discussed and decisions made on the best operations and water management scenarios for both species combined. From our perspective, even if the *O. mykiss* model in its present configuration could be improved to address the shortcomings discussed in Section 5, the model is still primarily a rainbow trout model that is not useful to NOAA Fisheries as a steelhead recovery tool.

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Appendix A
Letter to Steve Edmundson (NOAA Fisheries) and Response

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ANCHOR QEA

May 18, 2020

Mr. Steve Edmundson
FERC Branch Chief
NOAA Fisheries
California Central Valley Office
650 Capitol Mall, Suite 5-100
Sacramento, CA 95814

Re: Request for Additional Information on the Tuolumne River Chinook Salmon and *Oncorhynchus mykiss* Population Models

Dear Steve,

The following questions arose while conducting a Third-Party Review of the Tuolumne River Chinook Salmon and *Oncorhynchus mykiss* Population Models (Stillwater Sciences 2017a,b) for which we seek additional clarification. The models were developed for Turlock Irrigation District (TID) and Modesto Irrigation District (MID) by Stillwater Sciences, Berkeley, California. Most of the questions pertain to the Chinook Salmon Population Model, whereas the last two questions address aspects of the *Oncorhynchus mykiss* Population Model. Please forward this letter to the appropriate parties and request that our questions be addressed.

1. Page 4-5, Figure 4.1-4 shows the cumulative proportion of total Chinook salmon spawning activity distributed by spawning area per the approximate river mile. The text around this figure suggests that this distribution and the associated Equation 1 were used in the model to distribute female spawners along the river. Please verify this is how the model handles spawner distribution. Also, please identify if any other factors affecting spawner distribution are incorporated into the model. For example, at higher escapement levels do a higher percentage of spawners distribute downstream as suggested in McBain and Trush (2004), or is the same distribution used for all escapement levels?

2. Page 4-10, fry movement:

   - What is the basis for assuming that 30% of all emergent fry emigrate from the Tuolumne River? Also, please verify our understanding that this is a constant in the model under all conditions.
   - Please verify our interpretation that these fry emigrants are treated as mortality to the population; if our understanding is correct, please explain the rationale behind this assumption.

- The remaining fry (70%) are "assumed to be displaced for a period of 30 minutes." What is the basis for selecting 30 minutes, what is the purpose of this assumption, and how is it used in the model?
- Near the bottom of the page it states: "To account for movement at other flows, these rates were represented as a daily movement probability of 0.05 d-1 using the same 2-hr movement period and velocity estimate as applied to newly emergent fry (Equation 4)."
  - Please indicate what the 2-hour movement period is referring to? We have not found any mention of this elsewhere in the report that explains it, including the description of Equation 4.

3. Pages 4-15 and 4-16, juvenile movement:

- "Juvenile emigration prior to smoltification is not assumed to occur." What is the basis of this assumption? A rearing-downstream migration pattern is commonly observed by ocean-type Chinook salmon parr, more or less continuously, in rivers elsewhere (e.g., Nicholas and Hankin 1988; Healey 1991; Coutant and Whitney 2006).
- The same 2-hour movement period as mentioned above for fry seems to come into this; it states: "To account for these seasonal movements at higher flows, movement rates were represented as a daily movement probability initially estimated at 0.01 d-1 followed by a movement period of 2 hrs and velocity estimate from Equation 4. For areas with juvenile densities in excess of habitat carrying capacity, juvenile movement is initiated using the same 2 hr movement period and velocity estimates as for daily movements above."
  - Please explain this 2-hour period, how it works, and its purpose. We did not see an explanation of it in the report.
  - The description of the parr rearing pattern suggests that many parr (up to the carrying capacity) rear in the model in a more or less stationary location in the river until they achieve a minimum length of 70 mm and begin their smolt migration. Please clarify if this interpretation is correct.
- In the model, what happens to the parr that would move all the way to the bottom of the river and that are still less than 70 mm in length? It appears these fish are counted as mortalities. Please confirm whether this interpretation is correct.

4. Page 4-25, Table 4.2-3:

- The value for the parameter "fry.migr.mrate" is listed as being 5.408 days^{-1}. We interpret this to mean that 5.408 fry die per day during their migration. Please verify this is the correct interpretation or provide the correct interpretation of this rate. Normally we would expect a mortality rate to be between values of 0 and 1.
- We do not have access to the unpublished TID/MID data used in deriving the "fry.migr.mrate" parameter value; please provide these data.

5. Page 4-26 and Table 4.2-4:

- The value for the parameter "juv.migr.mrate" is listed as being 0.1386 $days^{-1}$. We can interpret this to mean that 0.1386 juveniles die per day, or a mortality rate of 13.86% is applied per day. Please clarify how this value should be interpreted.
- We do not have access to the unpublished TID/MID data used in deriving the "juv.migr.mrate" parameter value; please provide the data used to develop this value.
- Under smolt.fraction, please clarify how the 0.9 value is applied, i.e., to what?

6. Page 4-27:

- Middle: What is meant that the model user defines the length of time that displaced fish will travel downstream? This suggests that how this model input is defined is used as a type of calibration knob in the model, whereby the user calibrates to some number of resultant smolts. Please clarify this interpretation is correct and explain how this model input is used.
- Bottom: The text reads "Rather than applying temperature limits for smoltification, the model assumes a fixed proportion of smolt ready individuals ("smolt.fraction") will continue rearing (i.e., over-summer) to become yearling smolts in the following year." Please explain what happens to the 10% of juveniles that do not smolt as subyearlings and then continue to rear to become yearling smolts. For example, are they counted as yearling smolts and, if so, what survival rates are applied to estimate their abundance?
- For parr that are not displaced (i.e., they do not move), are they exposed to predator mortality and background mortality or are they only subjected to the background mortality? The text suggests these fish are not exposed to predator mortality; please verify this interpretation is correct.

7. Page 4-28, model calibration:

- Please identify the number of female spawners and fecundities applied in the calibration steps.

8. Page 4-29, model validation:

- Please identify the number of female spawners and fecundities applied in the validation steps.

9. Pages 5-8 and 5-9:

- Please provide all of the modeling output used to construct each graph in Figure 5.3-1 on page 5-9. We will reconstruct the graphs in a more conventional manner to facilitate understanding.

- Please provide the criteria used to determine which parameters shown in the charts in Figure 5.3-1 were determined to be significant.

10. Page 2-4, Attachment A (Stillwater Sciences 2017a), states "High levels of predation-related mortality have been documented in direct surveys by the Districts, in multi-year smolt survival tests and by comparisons of juvenile passage at upstream and downstream rotary screw trap monitoring locations." The only information related to smolt survival testing we have located was one year of study in 2012 using acoustically tagged hatchery-origin Chinook salmon (FISHBIO 2013). Given that "multi-year smolt survival tests" is plural, we may have not accessed all relevant studies. Please identify any additional reports of smolt survival tests that document high levels of predation-related mortality.

11. Page 2-6, Attachment A, Stillwater Sciences (2017a) states: "To account for the large increase in potential habitat at overbank locations, predation risk was assumed to be inversely proportional to wetted area at flows above 1,000 cfs. The model uses a mortality multiplier that is inversely proportional to wetted width within each reach. The flow-dependent mortality is scaled to equal 1.0 at 1,000 cfs discharge." Please explain the meaning of mortality being scaled to 1.0 at 1,000 cfs. For example, one could interpret this to mean that a mortality rate of 100% is applied when flow is at and above 1,000 cfs.

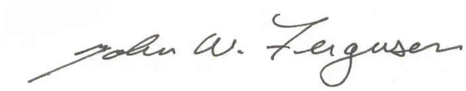
12. Please provide the data used in Figure 2.4-3, Attachment A (Stillwater Sciences 2017a).

13. Please clarify whether the models assume that survival-to-emergence values for new gravel patches (50% for Chinook salmon and 70% for *O. mykiss* as derived for the alternatives modeling [TID/MID 2019]) are persistent. If the models assume survival-to-emergence decreases over time due to fine sediment inputs from tributaries (e.g., patches downstream from Dominici Creek) please identify the changes over time used.

14. Please provide the modeling output used to construct Figures 5.2-1 to 5.2-4 on pages 5-5 to 5-8 of Stillwater Sciences (2017b).

Thank you for your attention to this request. A phenomenal amount of information has been developed and an impressive amount of work has gone into the development of the two models. Having clarity on these questions will help inform our understanding of how the models were constructed and function. Please extend our appreciation to scientists at Stillwater Sciences, TID, and MID, for responding to our questions.

Sincerely,



John Ferguson
Principal Fisheries Scientist

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Stillwater Sciences

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TECHNICAL MEMORANDUM

DATE: July 3, 2020

TO: Michael Cooke, Turlock Irrigation District

FROM: Noah Hume and Peter Baker, Stillwater Sciences

SUBJECT: Request for Additional Information on the Tuolumne River Chinook Salmon and *Oncorhynchus mykiss* Population Models

Dear Michael

We have reviewed the information request letter from NMFS (email from Steve Edmondson to Steve Boyd dated May 20, 2020) to support a Third-Party Review of the *Tuolumne River Chinook Salmon Population Model Amended Study Report* (Amended Report)(Stillwater Sciences 2017a) and *Oncorhynchus mykiss Population Amended Study Report* (Stillwater Sciences 2017b). To support the work of model reviewers retained by NMFS, we have developed responses to questions in the letter and requests for source data used in calibration, validation, and testing of the Tuolumne River Chinook (TRCh) and Tuolumne River *O. mykiss* (TROm) models that were developed as part of the ongoing FERC relicensing process for the Don Pedro Project. The following source files are available for download at the FTP link listed below:

- `TRCh calibration.data.zip` – Rotary Screw Trap (RST) data used in calibrating movement probabilities and migration mortality parameters, respectively for Chinook salmon fry (Question 4, bullet 2) and for juveniles (Question 5, bullet 2)
- `Sensitivity_TRCh33.xlsx` - TRCh Model Sensitivity Testing Results (Question 9)
- `TRCh3.3_rst_comparisons.xlsx` – TRCh model estimates of smolt productivity in comparison to those based upon RST monitoring (Question 12)
- `Sensitivity_TROm32.xlsx` – TROm Model Sensitivity Testing Results (Question 14)

https://ftp.stillwatersci.com
Login: NMFS_Review
Password: TRCh2019

As described in a June 17, 2020 FERC submission by the Districts (Accession 20200617-5172) a coding error was recently discovered in the TRCh and TROm models which affects the allocation of juvenile fish between the floodplain and the main channel. In addition to revising recent scenario results that accompany the June 17 filing, we have re-run the calibration, validation, and sensitivity testing results included in the Amended Report (Stillwater Sciences 2017a). The updated results included in the FTP folder reflect small increases in smolt productivity across all scenarios as noted in the June 17, 2020 FERC submission. The remainder of this memorandum provides responses to the questions in the NMFS letter in their original order of presentation.

Responses to May 20, 2020 Information Requested on the Tuolumne River Chinook Salmon and Oncorhynchus mykiss Population Models

1. ***Spawner Distribution*** *– "Page 4-5, Figure 4.1-4 shows the cumulative proportion of total Chinook salmon spawning activity distributed by spawning area per the approximate river mile. The text around this figure suggests that this distribution and the associated Equation 1 were used in the model to distribute female spawners along the river. Please verify this is how the model handles spawner distribution. Also, please identify if any other factors affecting spawner distribution are incorporated into the model. For example, at higher escapement levels do a higher percentage of spawners distribute downstream as suggested in McBain and Trush (2004), or is the same distribution used for all escapement levels?"*

<u>**Response:**</u> Yes, the TRCh model uses Equation 1 in the Amended Report to distribute female spawners along the river, with redd locations also affected by the relative availability of usable gravel areas as well as the presence of actively defended redds. Spawning habitat is represented at the level of individual gravel patches within size ranges suitable for Chinook salmon (or *O. mykiss*) spawning (TID/MID 2013a). The usable proportion of these areas relies upon physical habitat (PHABSIM) modeling reviewed by resource agencies (Stillwater Sciences 2013a) and is scaled by the relative proportion of modeled weighted usable area (WUA) within each model reach compared to the modeled WUA corresponding to flows observed during field mapping of spawning gravels (TID/MID 2013a).

Regarding downstream spawning habitat use at higher escapement levels, yes this is captured by the model and again depends upon the relative availability of usable gravel area as well as the total area of actively defended redds. As described in Section 4.1.1.2 of the Amended Report, individual spawners are directed to gravel patches with water temperatures below 16°C (60.4°F) by a random draw, with probabilities proportional to the undefended area scaled by the physical habitat modeling approach above as well as the river mile "preference" function described by Equation 1 of the Amended Report. It should be noted that because of the preference for upstream gravels discussed above, some level of redd superimposition occurs at all escapement levels as documented by detailed mapping and emergence trapping conducted in 1988 (TID/MID 1997b) as well as more detailed GPS based redd mapping conducted in 2012 (TID/MID 2013b).

2. ***Fry Movement*** *– "Page 4-10, fry movement:*
    a. *What is the basis for assuming that 30% of all emergent fry emigrate from the Tuolumne River? Also, please verify our understanding that this is a constant in the model under all conditions.*

<u>**Response:**</u> Although not described in the Amended Report, the basis for the 30% proportion of fry emigrants is the observation that large proportions (40-50%) of smaller fry (<35 mm FL) pass the Waterford (RM 29.5) RST with almost no larger fry (40-50 mm FL) observed (See long-term frequency distributions in Figure 1). Total passage at the downstream Grayson (RM 3.5) RST is lower than at Waterford and we cannot readily

estimate how many fry are rearing at intermediate locations between the two traps. Nevertheless, similar fork length distributions at both traps indicate large numbers of fry emigrate out of the lower Tuolumne soon after emergence (Figure 2). Approximately 30% of all fry-sized juveniles pass the Grayson RST at a size < 33 mm FL. The low representation of larger fry (40-50 mm) at both locations also indicates large numbers of fry emigrate out of the lower Tuolumne soon after emergence. As a regional comparison, in emigration monitoring of Fall-run Chinook salmon from the lower American River between 1995-1999, smaller (yolk-sac) fry typically emigrating in January made up approximately 23% of season-long fry passage (Snider and Titus 2002).

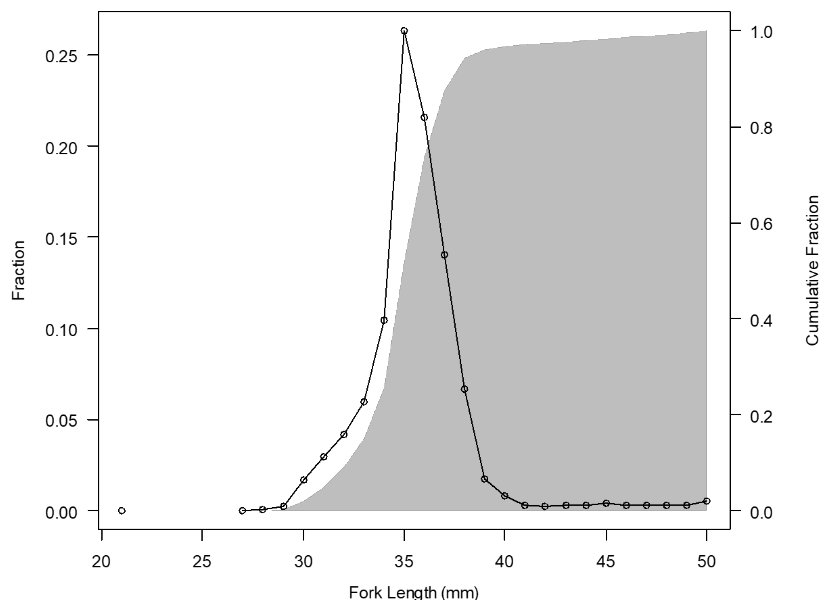

Figure 1. Fraction of Chinook salmon Fry < 50mm FL passing Waterford (RM 29) RST (2006-2012, 2015-2016, 2018)

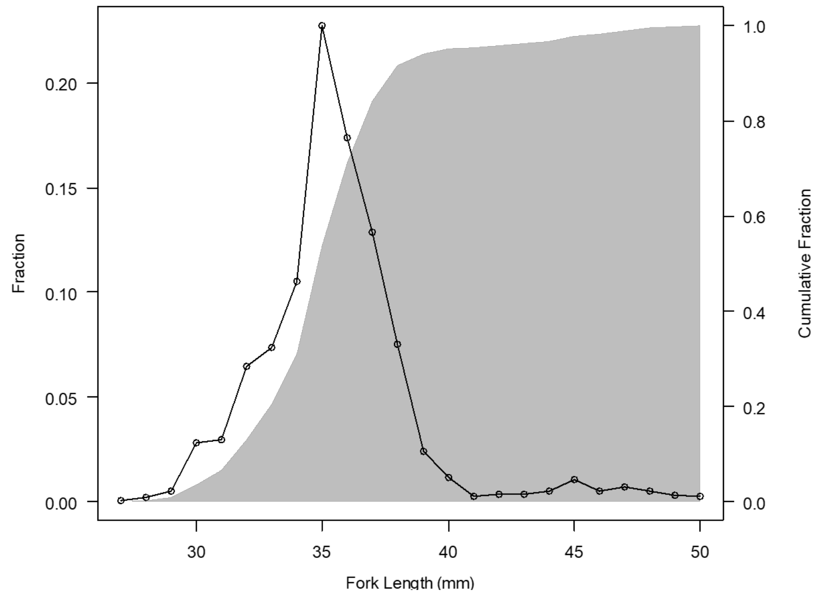

Figure 2. Fraction of Chinook salmon Fry < 50mm FL passing Grayson (RM 3.5) RST (2006-2012, 2015-2016, 2018)

b. "Please verify our interpretation that these fry emigrants are treated as mortality to the population; if our understanding is correct, please explain the rationale behind this assumption."

<u>Response:</u> Rearing fry-sized fish that are displaced downstream of Grayson (RM 5.2) RST and out of the Tuolumne River are not counted as mortalities and are also not counted towards later smolt emigration totals by the TRCh model. As stated above, 30% of all fry are classified as voluntary emigrants upon emergence, which drift downstream with the current until they either die or exit the river. Although the model can report fry totals reaching the confluence with the San Joaquin River, because as the TRCh model was designed to represent only in-river life stages in the approved FERC study plan, rearing downstream of the Tuolumne River is not simulated.

c. "The remaining fry (70%) are 'assumed to be displaced for a period of 30 minutes.' What is the basis for selecting 30 minutes, what is the purpose of this assumption, and how is it used in the model?"

<u>Response:</u> Fry movement parameters were fitted to reproduce juvenile seining time and space distributions included in Attachment C of the Amended Report. For the remaining 70% of fry that are simulated to rear in the Tuolumne River, rearing fry can become "displaced" from secure habitat, in which case they are carried downstream with the current for some time before re-establishing themselves. This time is randomly chosen for each fish as it becomes displaced, from a log-normal distribution with a mean of 30 minutes and a c.v. of 1. At each timestep, all fry newly emerged in that timestep, and all fry in excess of the local carrying capacity determined by density parameters and usable habitat area estimates, are displaced. Displacement of fry from otherwise secure habitat is represented as a Poisson process: the probability of an individual becoming displaced during a time interval Δt is $1 - \exp\left(-0.05\Delta t\right)$ (about 4.8 % per day). Because either the movement periods or displacement probabilities may be changed to calibrate to the seasonal seining distributions for the Tuolumne River shown, alternative assumptions regarding movement periods would necessarily require corresponding changes in the fitted displacement probabilities.

> d. *"Near the bottom of the page it states: 'To account for movement at other flows, these rates were represented as a daily movement probability of 0.05 d-1 using the same 2-hr movement period and velocity estimate as applied to newly emergent fry (Equation 4).' Please indicate what the 2-hour movement period is referring to? We have not found any mention of this elsewhere in the report that explains it, including the description of Equation 4*

<u>Response:</u> This appears to be a typographical error in the Amended Report as 30-minutes (0.0208 days) was the displacement period used for fry in the calibrated TRCh model (See Table 4.2-3).

3. ***Juvenile Movement*** – *"Pages 4-15 and 4-16, juvenile movement:*
   a. *"'Juvenile emigration prior to smoltification is not assumed to occur.' What is the basis of this assumption? A rearing-downstream migration pattern is commonly observed by ocean-type Chinook salmon parr, more or less continuously, in rivers elsewhere (e.g., Nicholas and Hankin 1988; Healey 1991; Coutant and Whitney 2006)."*

<u>Response:</u> This is incorrectly stated in the Amended Report and refers to the early emigration analogue for fry when a large proportion of fry sized juveniles voluntary emigrate. Although no such early dispersal mechanism is included for parr-sized juveniles and season-long RST monitoring at Grayson indicates that very few parr-sized (50-70 mm FL) fish emigrate from the Tuolumne River (See long-term frequency distributions in Figure 3), the TRCh model simulates low levels of parr emigration by drift and through displacement at higher densities. Consistent with the migration patterns referenced in the question, juvenile migration is represented in the same way as for rearing fry but using different parameter values to match seasonal seining distributions (Amended Report Attachment C) and RST passage estimates.

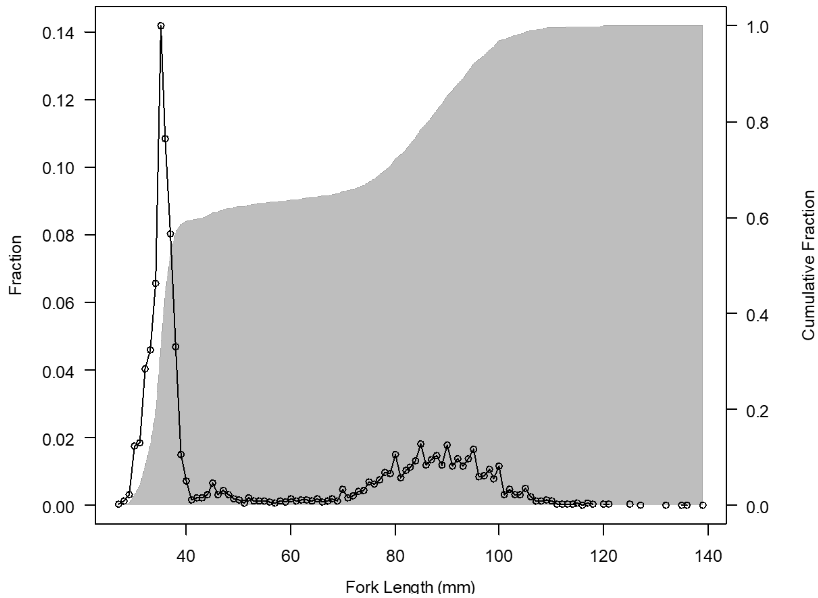

Figure 3. Fraction of all Chinook salmon juveniles passing Grayson (RM 3.5) RST (2006-2012, 2015-2016, 2018)

b. *"The same 2-hour movement period as mentioned above for fry seems to come into this; it states: 'To account for these seasonal movements at higher flows, movement rates were represented as a daily movement probability initially estimated at 0.01 d^{-1} followed by a movement period of 2 hrs and velocity estimate from Equation 4. For areas with juvenile densities in excess of habitat carrying capacity, juvenile movement is initiated using the same 2 hr movement period and velocity estimates as for daily movements above.' Please explain this 2-hour period, how it works, and its purpose. We did not see an explanation of it in the report."*

Response: For the pages being discussed, this mechanism was used with maximum rearing density parameters to simulate displacement events for fish in excess of local carrying capacity within a model reach. Rather than a 30-minute movement period used for fry, the mean dispersal time for displaced juveniles is 2 hours, and the probability of an otherwise secure individual becoming displaced during a time interval Δt is $1 - \exp{(-0.01\Delta t)}$ (about 1% per day). As with fry discussed above, daily juvenile movement parameters were fitted to reproduce juvenile seining distribution information from Attachment C of Amended Report. Assuming longer movement periods would necessarily require lower displacement probabilities.

c. *"The description of the parr rearing pattern suggests that many parr (up to the carrying capacity) rear in the model in a more or less stationary location in the river until they achieve a minimum length of 70 mm and begin their smolt migration. Please clarify if this interpretation is correct."*

Response: While the daily movement probabilities of parr-sized fish are much lower than that of fry and parr-sized fish accounts for a small proportion of season long juvenile passage at the Grayson (RM 5.2) RST (Figure 3), downstream "drift" is modeled to occur by TRCh based upon the movement periods (e.g., 2 hr for parr-sized fish) and velocities estimated from discharge and hydraulic geometry relationships based upon typical cross-sections in various reaches. For fish that are simulated to move, typical distances travelled range from 0.02 mi/day at 300 cfs to 0.1 mi/day at 5,000 cfs.

d. "In the model, what happens to the parr that would move all the way to the bottom of the river and that are still less than 70 mm in length? It appears these fish are counted as mortalities. Please confirm whether this interpretation is correct."

Response: As with fry, rearing parr-sized fish that pass the downstream Grayson (RM 3.5) RST and out of the Tuolumne River are not counted as mortalities but do not contribute to later smolt emigration totals and estimates of smolt productivity (smolts per female spawner) from the Tuolumne River. Alternative productivity metrics such as total juvenile passage per spawner could be used to account for these fishes' contributions to Tuolumne River production. Note that following the development of the Consultation Process for several studies conducted under the FERC Integrated Licensing Process, the metric of smolts/female spawner was proposed during Consultation Workshops conducted with relicensing participants in 2012.

4. ***Fry mortality rates –*** *"Page 4-25, Table 4.2-3:*
   a. The value for the parameter 'fry.migr.mrate' is listed as being 5.408 days^{-1}. We interpret this to mean that 5.408 fry die per day during their migration. Please verify this is the correct interpretation or provide the correct interpretation of this rate. Normally we would expect a mortality rate to be between values of 0 and 1."

Response: Most processes in the model are parameterized by instantaneous rates: an instantaneous rate of λ (in units of 1/day) corresponds to a rate of $1 - \exp(-\lambda \Delta t)$ over a time period of Δt days. Thus the parameter for fry migration mortality (fry.migr.mrate) value of 5.408 days^{-1} corresponds to a daily mortality rate of 99.55 %/d. Note that these rates are only for "displaced" individuals, and so will usually only be applied to fractions of a day and so the mortality rate applies to a small fraction of the total juvenile rearing population. As described in Section 2.2 of Attachment A in the Amended Report, the "mrate" and "migr.mrate" parameters are reach-specific and proportional to observed predator distributions in historical snorkel surveys. Reach specific mortality parameters for both fry and juvenile (parr-sized) Chinook salmon are provided in Table 1 below.

Table 1.Fitted reach specific instantaneous mortality rates of Chinook salmon juveniles

Reach	Instantaneous mortality rate (1/day)			
	Fry		Juvenile	
	mrate	migr.mrate	mrate	migr.mrate
LaGrange dam to OLGB	0.000019	0.09	0.000019	0.004
OLGB to TLSRA	0.00023	1.17	0.00023	0.05
TLSRA to Hickman Bridge	0.0011	5.41	0.0011	0.22
Hickman Bridge to Charles Road	0.0055	27.38	0.0055	1.10
Charles Road to Legion Park	0.0087	43.68	0.0087	1.75
Legion Park to Riverdale Park	0.0080	39.97	0.0080	1.60
Riverdale Park to Shiloh Bridge	0.0082	41.18	0.0082	1.65
Shiloh Bridge to mouth	0.0092	45.77	0.0092	1.83

b. *"We do not have access to the unpublished TID/MID data used in deriving the 'fry.migr.mrate" parameter value; please provide these data."*

Response: Rotary screw trapping summary data is included in annual FERC monitoring reports (e.g., Sonke and Fuller 2013). We have attached expanded juvenile passage data at the Waterford (RM 29) and Grayson (RM 5.2) RSTs (see `calibration.data.zip`) that was used in fitting mortality rates for the water years 2006-2013 (See FTP Folder). The expansion factors used to transform from daily RST catch to daily passage estimates were based upon re-analysis of historical RST monitoring data (Robichaud and English 2017).

5. ***Juvenile mortality rates –*** *"Page 4-26, Table 4.2-4:*
   a. *"The value for the parameter 'juv.migr.mrate' is listed as being 0.1386 days^{-1}. We can interpret this to mean that 0.1386 juveniles die per day, or a mortality rate of 13.86% is applied per day. Please clarify how this value should be interpreted."*

Response: As with fry movement parameters, an instantaneous mortality rate of λ (in units of 1/day) corresponds to a rate of $1 - \exp(-\lambda\Delta t)$ over a period of Δt days. Thus, the parameter for juvenile migration mortality (`juv.migr.mrate`) value of 0.1386 d^{-1} corresponds to a daily mortality rate of 12.94 %/d for the amount of time each fish moves within a day. As described in Section 2.2 of Attachment A in the Amended Report, the "mrate" and "migr.mrate" parameters are also reach-specific and proportional to observed predator distributions in historical snorkel surveys. Table 1 presents reach specific mortality parameters for juvenile (parr-sized) Chinook salmon.

   b. *"We do not have access to the unpublished TID/MID data used in deriving the 'juv.migr.mrate' parameter value; please provide the data used to develop this value."*

Response: For RST data applicable to juvenile mortality parameters see response to 4.b above.

c. *"Under smolt.fraction, please clarify how the 0.9 value is applied, i.e., to what?"*

Response: Based upon observations of rearing Chinook salmon during summer snorkel surveys conducted during July of most years (e.g., Stillwater Sciences 2013), we have assumed 10% of all fry reaching the parr-size threshold (>50 mm FL) are classified as voluntary summer residents in the TRCh model. The remainder are potential smolts when they cross the minimum smolt-size threshold (>70 mm FL). In addition, any potential smolts which are still alive and have not emigrated by the end of June are also converted to summer residents. Although there is some observations of yearling-size smolt emigration in annual RST monitoring reports (e.g., Sonke and Fuller 2013), the TRCh model does not currently simulate over-summering or potential yearling smolt emigration.

6. ***Juvenile Rearing –*** *"Page 4-27:*
   a. *"Middle: What is meant that the model user defines the length of time that displaced fish will travel downstream? This suggests that how this model input is defined is used as a type of calibration knob in the model, whereby the user calibrates to some number of resultant smolts. Please clarify this interpretation is correct and explain how this model input is used."*

Response: Downstream movement of fry and juvenile Chinook was simulated using an assumed daily displacement period (`juv.displace.time.mean`) with movement probabilities (`juv.displace.rate`) set by calibration to match observed RST passage timing. While no specific statement could be found containing "user defines", whole model calibration was accomplished by changes in the displacement rate and mortality rate parameters. Accordingly, the model may potentially be recalibrated by the end-user through changes in other parameters in the file `parameters.txt` included with the model code. Although some constants internal to the TRCh growth submodel are embedded within the model code, all other parameters in the model are visible to (and potentially changeable by) the model user. Reach-specific values are typically the product of values from the habitat files (`GRAVELS_wua.csv`, `FRY_HAB_in-channel.csv`, etc.) using a global multiplier from the `parameters.txt` file. For the most part, the availability of the parameters file is for transparency, to allow model sensitivity testing, as well as to represent specific hypothetical interventions (e.g., installation of spawning barriers at specific locations and dates to limit redd superimposition, changes in egg survival-to-emergence to represent gravel cleaning or gravel augmentation, changes in maximum rearing density in response to LWD, etc.).

   b. *"Bottom: The text reads 'Rather than applying temperature limits for smoltification, the model assumes a fixed proportion of smolt ready individuals ("smolt.fraction") will continue rearing (i.e., over-summer) to become yearling smolts in the following year.' Please explain what happens to the 10% of juveniles that do not smolt as subyearlings and then continue to rear to become* *yearling smolts. For example, are they counted as yearling smolts and, if so, what survival rates are applied to estimate their abundance?"*

Response: For the fraction of over-summering juveniles and potential for yearling smolts, please see response to 5.c above.

c. *"For parr that are not displaced (i.e., they do not move), are they exposed to predator mortality and background mortality or are they only subjected to the background mortality? The text suggests these fish are not exposed to predator mortality; please verify this interpretation is correct."*

Response: Yes, this interpretation is correct. "Predator" or movement mortality applies only to fish that are displaced. Note that the TRCh model does not explicitly represent predation as it relates to encounters between predators and rearing salmon. Instead, the model calculates "mortality" to match observed RST passage data through calibration. The main distinction in the model is between mortality experienced by migrating fish (displaced fry and juveniles, and emigrating smolts) and mortality experienced by fish residing in fixed locations. All rearing fry and juveniles are subjected to a daily "background" mortality, governed by mortality "mrate" parameters, to represent unmodeled sources (e.g., avian predation, disease, etc.). However, only migrating fish are exposed to "migration" mortality, governed by "migr.mrate" parameters.

7. ***Calibration –*** *"Page 4-28, model calibration:*
Please identify the number of female spawners and fecundities applied in the calibration steps."

Response: The model is initialized with a *population* of spawners rather than a *number* of spawners. Each spawner record specifies the gender, arrival date, and either length or age of an individual adult. As described in Section 4.1.1.2 of the Amended Report, the fecundities of females are calculated from their lengths or estimates of length based on age using data presented in Loudermilk et al. (1990). If lengths (in mm) are available, the fecundity is calculated as below:

$$\text{Eggs} = \min\left(\max\left(-6138.91 + 15.845 * \text{Length}, 1784\right), 9707\right)$$

The calibration/validation spawner population attributes are summarized in Table 2. Note that the spawner data used in the calibration/validation for 2009-2010, 2010-2011, 2011-2012, and 2012-2013 used initial populations extracted from the RM 24.5 counting weir data which includes genders and sizes (e.g., Wright et al. 2013). For the 2006–2007, 2007–2008, and 2008–2009 seasons, initial populations were synthesized to match the CDFW reported run sizes, timings, and spawning totals by river section (e.g., TID/MID 2011). The genders and sizes were drawn from the same distributions in all years (2006-2009), based on the genders and sizes of coded-wire-tagged fish recovered in the Tuolumne River (from the PFMC RMIS database) over the period of record. The arrival timing for each year was assumed to follow either the arrival dates at the counting weir or were "synthesized" using a normal distribution fitted to the weekly CDFW spawner survey live count data for that year.

Table 2. Summary of initial spawner populations used in calibration and validation of the TRCh model

season	arrival timing	Count		mean length (mm)		mean fecundity
		female	male	female	male	(eggs / female)
2006–2007	synthesized	308	317	763	725	5,955
2007–2008	synthesized	79	132	830	869	7,008
2008–2009	synthesized	216	156	763	867	5,956
2009–2010	weir	100	199	618	603	3,816
2010–2011	weir	423	395	670	675	4,659
2011–2012	weir	748	2,159	616	584	3,665
2012–2013	weir	868	1,328	648	592	4,187

8. ***Validation –*** *"Page 4-29, model validation:*

   Please identify the number of female spawners and fecundities applied in the validation steps."

Response: For the summary information on female spawners used for validation, please see response to 7 above.

9. ***Sensitivity Analyses –*** *"Page 5-8:*
   a. *"Please provide all of the modeling output used to construct each graph in Figure 5.3-1 on page 5-9. We will reconstruct the graphs in a more conventional manner to facilitate understanding."*

Response: As described in Section 5.3 of the Amended Report, sensitivity testing was conducted by running the TRCh model using sixteen scenarios and four values of each of the thirty parameters shown. Note that because of the model coding error disclosed in the FERC filing of June 17, 2020 we have provided an updated compilation of model sensitivity testing results in the file `Sensitivity_TRCh33.xlsx` (See FTP Folder).

   b. *"Please provide the criteria used to determine which parameters shown in the charts in Figure 5.3-1 were determined to be significant."*

Response: Sensitivity was assessed qualitatively by visual inspection to identify any slope deviations from horizontal in the sensitivity plots. In some cases, changes in smolt productivity slopes were apparent at unrealistic extremes of the sensitivity testing ranges (e.g., `spawn.wtemp.max, embryo.uuilt, fry.uuilt, juvenile.uuilt`).

Parameters with more consistent variation across the testing ranges were discussed in later sections in relation to factors potentially affecting the population.

10. ***Predation Related Mortality*** **–** *"Page 2-4, Attachment A (Stillwater Sciences 2017a), states 'High levels of predation-related mortality have been documented in direct surveys by the Districts, in multi-year smolt survival tests and by comparisons of juvenile passage at upstream and downstream rotary screw trap monitoring locations.' The only information related to smolt survival testing we have located was one year of study in 2012 using acoustically tagged hatchery-origin Chinook salmon (FISHBIO 2013). Given that 'multi-year smolt survival tests' is plural, we may have not accessed all relevant studies. Please identify any additional reports of smolt survival tests that document high levels of predation-related mortality."*

Response: As noted in Section 2.2 of Attachment A, information reviewed in the Synthesis Study (TID/MID 2013c) was used to support the statement regarding predation related mortality. Long-term paired-release smolt-survival tests conducted by the Districts (1987, 1990, 1994-2001) and relative comparisons of upstream and downstream smolt passage at the Waterford and Grayson RSTs (e.g., TID/MID 2012) do not include sampling of predatory fish species. Nevertheless, high rates of juvenile predation have been documented using direct sampling of stomach contents of predatory fish species (e.g., TID/MID 1992, McBain & Trush and Stillwater Sciences 2006, TID/MID 2013d).

11. ***Variations of Predation Mortality with Flow*** **–** *"Page 2-6, Attachment A, Stillwater Sciences (2017a) states: 'To account for the large increase in potential habitat at overbank locations, predation risk was assumed to be inversely proportional to wetted area at flows above 1,000 cfs. The model uses a mortality multiplier that is inversely proportional to wetted width within each reach. The flow-dependent mortality is scaled to equal 1.0 at 1,000 cfs discharge.' Please explain the meaning of mortality being scaled to 1.0 at 1,000 cfs. For example, one could interpret this to mean that a mortality rate of 100% is applied when flow is at and above 1,000 cfs."*

Response: As described in Section 2.2 of Attachment A, fitted mortality parameters between the upstream and downstream RSTs were rescaled to higher and lower values in each model reach based upon relative abundance of predatory fish species found in historical snorkel surveys within the lower Tuolumne River. Assuming that potential encounters between predatory fish and rearing Chinook juveniles are regulated by their relative densities, an additional scaling was implemented based upon inundated in-channel and floodplain areas at a given discharge. Although the bankfull discharges that correspond to the onset of floodplain inundation vary along the entire lower Tuolumne River, 1,000 cfs was chosen as a common discharge below bankfull at all locations. At flows above 1,000 cfs, the reach-specific (instantaneous) mortality rates are multiplied by the ratio of wetted area at 1,000 cfs to total wetted area. For example, when the total wetted area is twice the "in-channel area" (defined for this purpose as the area at 1,000 cfs), the mortality rates are reduced by half.

12. ***Model Validation Data*** *– "Please provide the data used in Figure 2.4-3, Attachment A (Stillwater Sciences 2017a)."*

Response: Model estimates of smolt productivity in comparison to those based upon weir counts and RST monitoring (Figure 2.4-3 of report Attachment A) are provided in the file `TRCh3.3_rst_comparisons.xlsx` (See FTP Folder).

13. ***Egg Survival-to-Emergence*** *– "Please clarify whether the models assume that survival-to-emergence values for new gravel patches (50% for Chinook salmon and 70% for O. mykiss as derived for the alternatives modeling [TID/MID 2019]) are persistent. If the models assume survival-to-emergence decreases over time due to fine sediment inputs from tributaries (e.g., patches downstream from Dominici Creek) please identify the changes over time used."*

Response: Yes, the assumed survival-to-emergence estimates of "new" gravel patches are persistent across the simulated water years. All survival-to-emergence parameters are assumed to apply to the entire incubation period, and all model simulations are interpreted as re-starts of the same initial conditions (of escapement and habitat conditions) under a set of 43 representative one-year hydrology conditions (rather than as single run of hydrology covering 43 consecutive years). Recognizing that changes in fine sediment accumulation in spawning gravels is a regular occurrence due to sediment loads from intermittent streams entering the Tuolumne River below La Grange Diversion Dam, examination of degradation of gravel quality over time could be accomplished by varying these model parameters over multiple simulations. Within-year changes in gravel quality currently cannot be represented without additional programming.

14. ***O. Mykiss Sensitivity Analyses*** *– "Please provide the modeling output used to construct Figures 5.2-1 to 5.2-4 on pages 5-5 to 5-8 of Stillwater Sciences (2017b)."*

Response: As described in Section 5.3 of the Amended *O. Mykiss Population Study* report (TID/MID 2017b), sensitivity testing was conducted by running the TROm model under multiple scenarios encompassing changes in population size, hydrology, as well as by systematic variation of the model parameters. We have provided a compilation of model results for these simulations in the file `Sensitivity_TRCh32.xlsx` (See FTP Folder).

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