

Submitted via electronic mail to fgc@fgc.ca.gov

April 4, 2024

The Honorable Samantha Murray
President
California Fish and Game Commission
P.O. Box 944209
Sacramento, CA 94244-2090

**RE: California Department of Fish and Wildlife Southern California Steelhead
(*Oncorhynchus mykiss*) Status Review Submission to Commission**

Dear President Murray,

The Association of California Water Agencies (ACWA) appreciates the opportunity to provide public comments to the California Fish and Game Commission (Commission) related to the status review of southern California steelhead (*Oncorhynchus mykiss*) (Status Review) submitted by the California Department of Fish and Wildlife (Department)—pursuant to Fish and Game Code § 2074.6. ACWA represents more than 460 public water agencies that collectively deliver approximately 90 percent of the water in California for domestic, agricultural, and industrial uses. ACWA and its members are invested in healthy watersheds and habitats that support robust populations of native fish and wildlife. However, ACWA has significant concerns regarding both the scientific basis for a listing determination and the potential impacts on public water agencies' ability to reliably provide water if southern California steelhead are listed as endangered pursuant to the California Endangered Species Act (CESA). Section 3, below, elaborates on these concerns.

1. Background

On June 14, 2021, California Trout (CalTrout) submitted a petition to the Commission to list southern California steelhead as an endangered species under CESA. On June 23, 2021, the Commission referred the petition to the Department for evaluation. On October 29, 2021, the Department submitted their evaluation report of the petition to the Commission. On April 21, 2022, the Commission accepted the petition for consideration. On May 13, 2022, the Commission provided public notice that southern California steelhead are a candidate species under CESA. On July 15, 2022, the Department noticed that it had initiated a 12-month Status Review of southern California steelhead and invited the public to submit comments, including data and other scientific information related to the species. In its Status Review, the Department

was required to evaluate the breadth of available scientific literature and develop a summary of the status of southern California steelhead. The Department was also required to seek independent peer review of its Status Review. On October 12, 2022, the Commission granted a six-month extension to the Department for their Status Review. On January 18, 2024, the Department submitted its Status Review to the Commission.

ACWA and its member agencies have been actively engaged throughout this process, submitting multiple comment letters to both the Commission and Department in response to the CalTrout petition, evaluation report of the petition, and Status Review for southern California steelhead.

2. Standard for Determination

The standard for listing is whether the species' "continued existence is in serious danger or is threatened by any one or any combination of the following factors: (1) Present or threatened modification or destruction of its habitat; (2) Overexploitation; (3) Predation; (4) Competition; (5) Disease; or (6) Other natural occurrences or human-related activities"—pursuant to 14 CCR 670.1(i)(1)(A). The Department's Status Review must be "based on the best scientific information available" and the Commission's decision whether to list must be "based solely upon the best available scientific information" pursuant to Fish and Game Code § 2074.6 and Fish and Game Code § 2070, respectively.

3. ACWA Comments

ACWA appreciates the mission of the Commission, which is to ensure that California will have abundant, healthy, and diverse fish and wildlife that thrive within dynamic ecosystems. Public water agencies are intimately involved in the management of watersheds and wildlife habitats and ACWA member agencies have become increasingly involved in the proactive resolution of fishery and other aquatic species resource management issues. ACWA has the following significant concerns regarding the petition to list southern California steelhead pursuant to CESA.

a. The Department's Status Review Does Not Incorporate the Best Available Science

While the Status Review assesses the status and trends of southern California steelhead rainbow trout¹ (Southern SH/RT), the Department evaluates sympatric populations of anadromous and resident *O. mykiss* separately. Because of this

¹ In the Status Review, the Department defines southern California steelhead as "all *O. mykiss* below manmade and natural complete barriers to anadromy, including anadromous and resident life histories". To accurately capture this life history variability, the Department uses "southern California steelhead rainbow trout" to describe the proposed CESA listing unit.

separate treatment, the reproductive contributions of sympatric resident spawners to the production of smolts and anadromous *O. mykiss* are not accounted for in measures of population status or the evaluation of long-term viability of southern California steelhead. In addition, the Department does not consider the potential contributions from above-barrier populations of resident *O. mykiss* to Southern SH/RT populations, resulting from the downstream migration of juvenile rainbow trout over barriers. While above-barrier *O. mykiss* are not included in the petition, a subset of that population may increase the effective population size or rescue below-barrier populations from extirpation, therefore improving the viability and persistence of Southern SH/RT.

This interchange between resident and anadromous fish populations, and the associated “rescue effect”, reduces the extinction risk of both groups and allows for recolonization should low steelhead abundance occur.² In their Viability Assessment for Pacific Salmon and Steelhead Listed Under the Endangered Species Act: Southwest, the National Marine Fisheries Service (NMFS) recognizes that “freshwater-resident (non-anadromous) forms of *O. mykiss* co-occur and appear to interbreed with the anadromous form in many populations” and concludes that “resident (nonanadromus) [sic] *O. mykiss* warrant consideration in managing for the anadromous life history.”³ Similarly, in October 2023, Judge James Chalfant expressed concerns during *United Water Conservation District v. California Fish and Game Commission*, acknowledging that “it may be true that an evaluation of rainbow trout [abundance and] its ability to produce [smolts] is required before [southern California steelhead] can be the subject of stage 2 protection as an endangered species.”⁴

The Population Trends and Abundance analysis in Chapter 4 of the Status Review also presents several flaws. First, it utilizes problematic trap data which (1) only account for individuals that are migrating or biologically motivated to move within the watershed (e.g., due to resource availability), (2) are limited to periods when flows allow for the installation and operation of traps—that is, high flow conditions may preclude trap operation when migration is most likely to occur, and (3) are not representative of the trapped portion of *O. mykiss* without a trap efficiency study. Trap efficiency studies are required to develop accurate population estimates from numbers of trapped fish. Unfortunately, the Status Review does not disclose or describe whether trap efficiency studies are available in connection with the different datasets.

Second, while the Status Review acknowledges additional data sources (e.g., snorkel surveys, video-based and surveillance system fish counts), which in some watersheds

² Boughton, D.A., et al. 2007. Viability criteria for steelhead of the South-Central and Southern California coast. NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-407.

³ NMFS. 2023. Viability assessment for Pacific salmon and steelhead listed under the Endangered Species Act: Southwest. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SWFSC-686. Page 155.

⁴ Case No. 22STCP02661. Page 9.

may more accurately characterize the overall *O. mykiss* population, they appear not to have been incorporated into the Population Trends and Abundance analysis consistently.

In addition to statistically inappropriate treatment of the trap data, many of the data presented in the Status Review were not analyzed appropriately. In Section 4.1, the evaluation erroneously compared trap data directly with snorkel survey/bankside observation data (instead of evaluating the different types of survey data separately), evaluated total fish counts per year (instead of fish counts per number of days of trap operation or per distances visually surveyed), and included zero values in some years when monitoring did not occur (instead of consistently excluding all years when monitoring did not occur). Furthermore, in Section 4.3's trend analysis, annual fish count data from the Santa Ynez, Ventura, and Santa Clara Rivers were inappropriately evaluated across the c. 1994 to c. 2021 timeseries without considering methodological changes that occurred within those years—which the Department noted in Appendix C of the Status Review.⁵

Finally, the Department's focus on a 5-year timeframe (i.e., 2013 to 2018) when discussing productivity in the Population Trends and Abundance analysis in Section 4.5 is non-representative and skews their conclusions. This timeframe coincides with the most recent extreme drought period and conditions associated with the loss of suitable spawning and rearing habitat, insufficient instream flows required for migration, diminished water quality, reductions in available food supply, and increases in direct mortality. While most populations do not have enough data available following the drought to determine if rebounding has occurred, the Department does note potential post-drought rebounding in the only population (i.e., Santa Ynez River) with a dataset through 2021. In NMFS' Southern California Steelhead Recovery Plan, Dr. David A. Boughton explains that "steelhead recovery as a form of human stewardship has to be judged over a broader timeline, with multi-year setbacks in population size considered to be a normal and expected event, and progress judged at the scale of multiple decades and even multiple human generations."⁶

b. Consider Information and Data That Use the Best Available Science to Assess the Viability of the Distinct Population Segment (DPS) in the Context of Threats to the DPS

Consistent with the Department's July 15, 2022, solicitation, various water agencies have shared information for the Department's Status Review. The information

⁵ Cramer, S.P. and Caldwell, L. 2020. Bias and consequences in attempts to estimate historic salmon abundance. *Canadian Journal of Fisheries and Aquatic Sciences*, 77(1):132-145.

⁶ National Marine Fisheries Service. 2012. Southern California Steelhead Recovery Plan. Southwest Region, Protected Resources Division, Long Beach, California. Page 5-1.

submitted contributes to the best available science and highlights the basis for ACWA's concerns with the potential listing of Southern SH/RT.

A new cohort-based life cycle simulation model (model), developed by Cramer Fish Sciences in collaboration with ACWA member agencies, includes the diverse and interrelated life history variants of *O. mykiss*. The model incorporates anadromous, below-barrier resident, and above-barrier resident sub-populations to evaluate population dynamics and assess extinction risk when resident *O. mykiss* are available to contribute to anadromous populations. When appropriately structured and parameterized, the model is a tool for evaluating these contributions and determining whether sympatric resident populations support long-term viability of southern California steelhead populations. The model demonstrates that the contribution of anadromous and resident (below- and above-barrier) life history variants and their connectivity can affect a population's trajectory, and that omitting them may not fully capture the DPS's long-term resiliency. Cramer Fish Sciences, ACWA, and collaborating member agencies met with the Department on December 12, 2023, to discuss and review the model, prior to the Department's submittal of the Status Review to the Commission.

Cramer Fish Sciences' model reflects existing literature indicating freshwater populations of both below- and above-barrier resident *O. Mykiss* improve the viability of the anadromous life history and contribute to the long-term persistence of the overall *O. Mykiss* population across the range of life histories it exhibits. Although anadromous spawners alone could support the DPS, the model predicted that southern California steelhead are always at or close to collapse without reproductive contributions from below- and above-barrier resident spawners under all conditions but the highest ocean survival scenarios. Depending on contributions to anadromous spawning populations in wet years, the resident life histories provide additional population stability and reduced extinction risk that should be accounted for when making regulatory determinations and setting recovery targets.

The model is supported by the extensive research conducted by ACWA member agencies, survey data, and the available scientific literature and fills a key data gap highlighted by water agencies in past comments and information submittals to the Commission and the Department throughout the petition process. The model is formulated using sound logic and consistent with prevailing practices, with its structure and default parameterization informed by the empirical data that align with the current scientific understanding. Therefore, the model—when combined with other data, analyses, and tools—constitutes the best available scientific information. As a consequence, the Department is obliged to utilize the model and model results to inform its Status Review, and the Commission is obliged to consider the model and model results to inform its ultimate listing decision.

c. Consider Ongoing Restoration and Recovery Activities That Contribute to Conservation and Reduce Threats to the Species

The Department, California Department of Transportation, California State Parks, U.S. Forest Service, County of Ventura, City of San Buenaventura, City of Santa Barbara, City of Carpinteria, City of Malibu, Cachuma Operation and Maintenance Board, Casitas Municipal Water District, United Water Conservation District, Santa Monica Mountains Resource Conservation District, South Coast Habitat Restoration, CalTrout, and many other organizations are currently engaged in significant ongoing restoration and recovery work throughout the DPS. Numerous small- and large-scale recovery actions have already been implemented by the agencies listed above while other actions are in the advanced planning phases. These actions include, but are not limited to:

- Robles Fish Passage Facility modifications on the Ventura River
- Matilija Dam Ecosystem Restoration Project on Matilija Creek
- Foster Park Fish Passage Improvement Projects on the Ventura River
- San Antonio Creek fish passage barrier removal
- Freeman Diversion Habitat Conservation Plan and fish passage improvements on the Santa Clara River
- VenturaWaterPure Program for Santa Clara River Estuary habitat improvements
- Rindge Dam decommissioning on Malibu Creek
- Hilton Creek fish passage barrier removal
- Quiota Creek fish passage barrier removals
- Salsipuedes Creek and El Jaro Creek Fish passage barrier structures
- Gaviota Creek fish passage barrier removal
- Tajiguas Creek fish passage barrier removals
- Arroyo Burro fish passage barrier removal and Mesa creek restoration project
- Mission Creek fish passage barrier removals
- Carpinteria Creek fish passage barrier removals
- Maria Ignacio Creek fish passage barrier removal
- Arroyo Hondo Creek Fish Passage Project
- Solstice Creek Fish Passage Restoration
- Malibu Creek fish passage barrier removal project and Malibu Lagoon restoration project
- San Juan Creek dams and fish passage barrier removals
- Trabuco Creek Fish Passage Project

These current and anticipated restoration and recovery actions are consistent with NMFS' Southern California Steelhead Recovery Plan and are anticipated to result in a measurable increase in *O. mykiss* abundance within the southern California DPS over a

reasonable timeframe.⁷ Large-scale recovery actions are underway or have already occurred in the neighboring south-central steelhead DPS (e.g., San Clemente Dam decommissioning, Los Padres dam fish passage design, Arroyo Grande Creek and watershed improvement projects) that may also aid in the recovery of the southern California steelhead DPS.

Some of these restoration and recovery actions have taken, and will continue to take, years to permit and implement. Some of these completed projects may take years to realize population recovery due to the natural stochasticity of populations and the complex chain of effects between the action and the population-level response. Consequently, prematurely dismissing the efficacy of restoration efforts resulting from the federal listing and NMFS' Southern California Steelhead Recovery Plan is unwarranted. Evaluating the success of this work will likely require a decades-long perspective because of the time required for planning and executing recovery projects, as well as realizing their benefits for the species. In addition, external factors such as precipitation patterns, ocean conditions, and stochastic events may cause annual fluctuations in *O. mykiss* abundance, even if the population experiences a positive growth rate over longer timescales. It is a disconcerting reality that a state listing of the population is likely to increase the time and cost incurred to implement restoration and recovery actions to benefit the population.

d. Consider That a State Listing Would Not Trigger Additional California Environmental Quality Act (CEQA) Evaluations or Afford Additional Protection Beyond that Provided by the Federal Endangered Species Act (FESA)

FESA already prohibits steelhead “take” by law, and the federal definition is wider ranging than the “take” definition under the Fish and Game Code (§ 86), and includes “to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect or attempt to engage in any such conduct,” 16 U.S.C. 1532(19), and “harm” is further defined as “an act which actually kills or injures wildlife. Such an act may include significant habitat modification or degradation where it actually kills or injures wildlife by significantly impairing essential behavioral patterns, including breeding, feeding, or sheltering,” 50 C.F.R. 17.3.

Effects to all special-status species and designated critical habitat are evaluated under CEQA. The Status Review, in Section 7.1.1, fails to explain that CEQA is already triggered if a project would affect southern California steelhead because the species is federally listed. In Section 11, the Status Review erroneously claims that: “Additional protection of Southern SH/RT following listing would also occur during required state and local agency environmental review under CEQA. CEQA requires affected public agencies to analyze and disclose project-related environmental effects, including

⁷ National Marine Fisheries Service. 2012. Southern California Steelhead Recovery Plan. Southwest Region, Protected Resources Division, Long Beach, California.

potentially significant impacts on endangered, threatened, and rare special status species. Under CEQA’s “substantive mandate,” state and local agencies in California must avoid or substantially lessen significant environmental effects to the extent feasible. With that mandate, and the Department’s regulatory jurisdiction generally, the Department expects related CEQA review will likely result in increased information regarding the status of Southern SH/RT in California as a result of pre-project biological surveys.”⁸ Because the species is already listed under FESA and it is presumed that “all juvenile *O. mykiss* in streams where listed steelhead occur are listed juvenile steelhead”, there would be no additional CEQA reviews or collection of biological information on the species’ status due to listing southern California steelhead under CESA.⁹

The Department is typically already included in interagency coordination and project evaluations through the Lake and Streambed Alteration Program, Fish and Game Code § 1600. Section 7(a)(2) of FESA, 16 U.S.C. 1536(a)(2), requires federal agencies to ensure actions are not likely to jeopardize the continued existence of a species or adversely modify its designated critical habitat. The Status Review claims that application of this section of FESA is limited in scope because it applies only to federal actions and areas under federal ownership; however, most or all projects physically affecting streams that support *O. Mykiss* require permitting and approval by the U.S. Army Corp of Engineers, which would trigger Section 7(a)(2). In addition, the take prohibition under FESA applies irrespective of whether there is a federal nexus.

Under FESA, for incidental take to be authorized, impacts to endangered species must be minimized and jeopardy of the species and/or adverse modification of critical habitat must be avoided. The only additional protection afforded by listing the species under CESA would be that impacts and take must be minimized or “fully mitigated”; however, this standard is tempered by the CESA requirement that the mitigation must be “roughly proportional” to the impact of the take, Fish and Game Code § 2081(b)(2). In sum, there is no evidence that CESA would provide additional protections for *O. mykiss* above and beyond that provided by FESA.

e. Minimize Impacts on Water Management and Programs That Benefit Southern California Steelhead

Designation of southern California steelhead as an endangered species could have significant impacts on water management operations in the region that are critical to public health and safety. Long-term water resilience and the successful

⁸ California Department of Fish and Wildlife. 2024. Report to the California Fish and Game Commission. California Endangered Species Act Status Review for Southern California Steelhead (*Oncorhynchus mykiss*). Sacramento, California. Page 142.

⁹ National Oceanic and Atmospheric Administration. Endangered and Threatened Species: Final Listing Determinations for 10 Distinct Population Segments of West Coast Steelhead, 71 Fed. Reg. Jan. 5, 2006. Page 841.

implementation of CESA requires that regulatory agencies collaborate with interested parties to develop an approach that accounts for the various and unique needs of the region and balances water supply reliability and ecosystem enhancement.

Steelhead listings under FESA, which already provides protection to the species as a matter of federal law, have resulted in substantial curtailments of water diversions and extractions in southern California coastal streams. A CESA listing could result in infeasible avoidance and minimization measures for water management and water facility operation activities occurring in streams populated or potentially suitable for future population by *O. mykiss*. In addition, instream flow mandates have the potential to diminish local water supplies at the same time the State is requiring local water agencies to reduce reliance on water supplies that flow through the Sacramento-San Joaquin Delta or are derived from the Colorado River. Regionally, this reduction in available water supply would have significant impacts including, but not limited to, increased overdraft of groundwater basins; reductions in water for municipal, agricultural, and industrial users; water quality degradation detrimental to human health (e.g., increased nitrate concentrations); reductions in agricultural production; job losses; and financial stress to disadvantaged communities and their water systems. More broadly, reductions in available water supply from local sources would place added stress on the State Water Project and other regional and state-level water infrastructure. A CESA listing would have significant impacts to water management, water agencies, and water users throughout the region.

These regulatory effects would impact ongoing or planned projects intended to protect and contribute to recovery of the DPS—such as fish passage projects, habitat restoration projects, and multi-benefit water supply projects designed to meet the state’s resiliency and sustainability goals. If the Commission decides to designate *O. mykiss* as an endangered species, water agencies will be subject to additional permitting that could delay projects, increase costs, and generate redundancies given that the species is already listed under federal law and given other federal, state, and local environmental protections. The Department is already a partner in federal consultation and recovery efforts and has developed site-specific protection measures through individual permits and agreements in collaboration with NMFS. In addition, a CESA listing could have unanticipated detrimental effects on southern California steelhead if water agencies are reluctant to implement watershed projects with the potential to benefit anadromous *O. mykiss* because of the possibility of incidental take. For example, the planned removal of the Matilija Dam in Ventura County has been delayed, in part, because of concerns over inadvertent take caused by the mass release of sediment into the Ventura River system as a result of the project.

Moreover, in order to allow the Department and other resource agencies to focus their efforts on the recovery of southern California steelhead, and to allow ACWA member agencies to commit resources to meaningful watershed projects that contribute to the recovery of the DPS, it would be prudent for the Commission to

exclude from the proposed listing coastal watersheds where the Department had previously identified concrete-lined flood control channels that present hydraulic (i.e., velocity) barriers to steelhead passage. These structures can extend many miles inland from the river mouth and have been recognized throughout California as barriers to successful upstream migration.

Public water agencies in the impacted central and southern coastal watersheds are working diligently to effectively manage limited water supplies and continue efforts to conserve the species, and they are doing so per the existing federal listing of *O. mykiss*. ACWA member agencies should be allowed to continue their work without an additional layer of regulations and prohibitions in watersheds that are not anticipated to ever provide passage for southern California steelhead. Great care should be taken during the listing process to ensure that existing watershed projects, that will ultimately benefit anadromous *O. mykiss* and other riparian species, are not frustrated by a CESA listing—which is indicated herein does not appear to be supported by the best available science. Managing drought emergencies and long-term climate change impacts requires close collaboration between local and state agencies to continue to provide safe, affordable, and reliable water to southern Californians, and the listing in its current form has the potential to frustrate required coordination.

Conclusion

ACWA appreciates the responsibility currently before the Commission in evaluating the petition and Status Review. There are many factors that will determine the current status of southern California steelhead and a thorough review and analysis of the best available science is needed. ACWA's members along California's South Coast are closely following this effort as the Commission's ultimate decision could have significant impacts on water management operations throughout the region and hinder their ability to provide water supplies to their diverse customers in one of the most densely populated parts of the country.

ACWA appreciates the opportunity to comment and the collaboration of Department and Commission staff. If you have any questions regarding these comments, please contact me at StephenP@acwa.com or (916) 669-2369.

Sincerely,



Stephen Pang
State Relations Advocate
Association of California Water Agencies

Cc: The Honorable Erika Zavaleta, Vice President, California Fish and Game Commission
The Honorable Darius Anderson, Member, California Fish and Game Commission
The Honorable Jacque Hostler-Carmesin, Member, California Fish and Game Commission
The Honorable Eric Sklar, Member, California Fish and Game Commission
Ms. Melissa Miller-Henson, Executive Director, California Fish and Game Commission
Mr. Scott Gardner, Wildlife Branch Chief, California Department of Fish and Wildlife
Mr. Dave Eggerton, Executive Director, Association of California Water Agencies
Ms. Cindy Tuck, Deputy Executive Director, Association of California Water Agencies

Appendix 1

Four Peaks Environmental Science & Data Solutions' Technical Memorandum

TECHNICAL MEMORANDUM

04/03/2024

TO: Stephen Pang, Association of California Water Agencies
FROM: Lucius Caldwell, Elizabeth Ng, and Grant Woodard, Four Peaks Environmental Science & Data Solutions
SUBJECT: Review of Cramer Fish Sciences Southern California Steelhead Life Cycle Model

Executive Summary

The distinct population segment of Southern California steelhead (*Oncorhynchus mykiss*) below impassible migration barriers is currently listed as Endangered under the federal Endangered Species Act (ESA). This federal ESA-listed population, which is managed by the National Marine Fisheries Service (NMFS), includes only anadromous *O. mykiss* and does not protect freshwater resident life histories. However, the interdependencies of sympatric resident and anadromous life histories was acknowledged by NMFS in their 2006 listing determination, and in 1997 NMFS had defined Southern California steelhead to include resident fish.

In 2021, California Trout petitioned the California Fish and Game Commission to list Southern California steelhead (including all *O. mykiss* below impassible barriers to migration) as an endangered species under the California Endangered Species Act. In an evaluation of this petition published in 2021, the California Department of Fish and Wildlife (CDFW) determined listing may be warranted. This prompted a full evaluation of the status of Southern California steelhead populations by CDFW in a January 2024 report.

The Association of California Water Agencies contracted with Four Peaks Environmental Science & Data Solutions (Four Peaks) to provide a critical review and evaluation of the 2024 CDFW Southern California Steelhead Status Report delivered to the California Fish and Game Commission (CDFW Report), as well as a Southern California steelhead life cycle model developed by Cramer Fish Services (CFS LCM). The CFS LCM was designed to address deficiencies in the current population viability assessments by CDFW and NMFS that only include anadromous spawners. The CFS LCM aims to estimate anadromous and freshwater resident Southern California *O. mykiss* dynamics more accurately by including the effects of both resident and anadromous life histories on anadromous population dynamics.

The CDFW Report provides a relatively comprehensive review of the current status of Southern California steelhead but has some key flaws. First, the underlying data used for some of the analyses in the CDFW Report are limited in terms of their duration, spatial extent, and completeness. These data gaps limit the quality of inferences that can be drawn from the resulting analyses. This issue of limited data availability is heightened by the omission of some key sources of available data. Additionally, some of the data presented in the report are not analyzed correctly. Specifically, some count data—which are indices of population abundance and not abundance estimates themselves—are presented as abundance data, resulting in an inaccurate estimate of abundance. Finally, the CDFW Report analyzes the freshwater resident and anadromous life histories separately, despite their documented

interbreeding and ability to give rise to one another, raising questions about the validity of their population viability assessment.

The initial draft of the CFS LCM provides a mechanism for assessing population dynamics when including the interrelated life histories of anadromous and freshwater resident *O. mykiss* populations both above and below barriers to migration. The structure of this model is logical, and the initial default parameterization is defensible and based on empirical data. However, it does have limitations that need to be addressed before it can be used to rigorously evaluate Southern California steelhead population dynamics. Notably, key life stage transition rates such as smolt rates and ocean survival are not parameterizable for individual life histories (anadromous versus resident). This does not allow for these rates to vary, as would be expected due to underlying genetic differences between the two life histories. Additionally, the fecundity parameter is not age-specific, even though fecundity tends to be highly correlated with fish size.

To evaluate the influence of certain key parameters, a sensitivity analysis of the CFS LCM was conducted by Four Peaks. The purpose of this effort was to determine the effects on population dynamics that may propagate through the model from inaccuracies around starting values for population size, fecundity rates, smolt rates, and ocean survival rates. Results from this effort indicated that population dynamics were relatively robust to the starting population size; however, fecundity, smolt rate, and ocean survival rates substantially influenced population dynamics, with higher values of the parameters increasing the long-term viability of the anadromous population. In general, anadromous spawners contributed more to the long-term viability of the anadromous population than resident spawners, though the extent was influenced by environmental conditions.

1 Introduction

1.1 Context

The Association of California Water Agencies has contracted with Four Peaks Environmental Science & Data Solutions (Four Peaks) to provide a critical review of documents related to a petition from California Trout (CalTrout) to list Southern California steelhead (*Oncorhynchus mykiss*) as an endangered species under the California Endangered Species Act (CESA) (CalTrout 2021). The petition notably includes freshwater resident *O. mykiss* (rainbow trout) below impassable barriers. In November 2021, the California Department of Fish and Wildlife (CDFW) published their evaluation of the petition to list Southern California steelhead/rainbow trout¹ (Southern SH/RT), which concluded that, “the petition action may be warranted,” (CDFW 2021). In May 2022, the California Fish and Game Commission (Commission) published a Notification of Findings indicating they accepted the petition for consideration (CFGF 2022), prompting CDFW to compile a Southern SH/RT status review to determine if the petition action is warranted.

In October 2023, United Water Conservation District (UCWD) challenged the Commission’s decision in court (UCWD v. California Fish and Game 2023). During this hearing, Hon. James C. Chalfant, Judge, stated that an evaluation of freshwater resident rainbow trout abundance and the ability of these

¹ To disambiguate the intended treatment of resident fish within the population proposed for listing under the CESA, CDFW refers to the population as Southern California steelhead rainbow trout.

freshwater resident fish to produce smolts (anadromous individuals) would be required to support a decision to protect Southern SH/RT as an endangered species. Chalfant also raised questions about the rate of smolting among freshwater resident rainbow trout and about precise estimates of rainbow trout population² abundance that would be needed before listing. These questions about abundance of freshwater resident fish, ability of freshwater resident fish to smolt, and the rate at which freshwater resident fish smolt are pertinent to the ongoing deliberations regarding Southern SH/RT listing.

In January 2024, CDFW published their status review, in which they stated, “The Department recommends that the Commission find the petitioned action to list Southern SH/RT as an endangered species to be warranted,” (CDFW 2024). This memorandum provides a review and evaluation of CDFW’s Southern California steelhead status review report (2024) and a review of a technical memorandum prepared by Cramer Fish Science describing a life cycle model (CFS LCM) developed to evaluate Southern California steelhead population viability (CFS 2024).³ The following specific objectives were defined to support this goal:

1. Summarize the key regulatory issues related to CESA-listing of Southern California steelhead
2. Review and critique the CDFW status report
3. Review, summarize, and critique the CFS technical memorandum

The remainder of this technical memorandum presents the following components:

- A summary of the current regulatory status of Southern California steelhead (Section 1.2)
- A summary of the petition to list (Section 1.3)
- Four Peaks’ review and evaluation of the CDFW Report (Section 2)
- Four Peaks’ review and evaluation of the CFS technical memorandum (Section 3), which includes an Executive Summary of this technical memorandum suitable for dissemination as a standalone document to brief interested parties in advance of future discussions (Section 3.1)
- Results from Four Peaks’ sensitivity analysis of the CFS LCM to evaluate the relative influence of model parameter assumptions on model predicted population dynamics for Southern California steelhead (Section 4)

1.2 Current Regulatory Status of Southern California Steelhead

The Southern California steelhead evolutionarily significant unit (ESU) was initially listed as endangered under the federal Endangered Species Act (ESA) in 1997 (NMFS 1997). At that time, the National Marine Fisheries Service (NMFS) listed only the anadromous form of *O. mykiss* within the stated range of Southern California steelhead (NMFS 1997, pg. 43938). In 2002, the southern range limit of Southern California steelhead was extended under the ESA listing (NMFS 2002). The initial 1997 decision by NMFS to list only anadromous *O. mykiss* has been followed in each subsequent listing: in 2006, the ESA listing

² Note that the term “population” is used throughout this document to refer to groups of individuals that, in some cases, exist at different hierarchical levels. For example, there is the worldwide population of steelhead, the Southern California steelhead population, populations of Southern California steelhead that exist within each basin, and populations of anadromous and resident fish within those populations of Southern California steelhead within each basin. To maintain readability and avoid introducing excessive terminology, no effort has been made throughout this document to disambiguate these groups except for cases in which a subpopulation is referred to in direct reference to its parent population.

³ “Viability” in this context implies less than 5% extinction risk over the next 100 years (see NMFS 2023b, pg. 16).

was further modified to relist the Southern California steelhead ESU as a distinct population segment (DPS), further distinguishing between the anadromous and resident forms of *O. mykiss* (NMFS 2006). In the 2006 listing, NMFS reiterated, “Within these geographic boundaries, we further conclude that the anadromous life form is markedly separate from the resident life form... We therefore are delineating... steelhead-only DPSs,” (NMFS 2006, pg. 848). In summarizing their status assessment leading to this 2006 listing, NMFS stated, “the BRT [*an expert panel of scientists from several Federal agencies including NMFS, FWS, and the U.S. Geological Survey*] concluded that the contribution of the resident life-history form to the viability of an *O. mykiss* ESU in-total is unknown and may not substantially reduce extinction risks to an ESU in-total,” (NMFS 2006, pg. 851). The current understanding, summarized in NMFS’s most recent Status Review, is that individuals of the resident life history do contribute to anadromous populations, although the degree to which this affects population dynamics remains unquantified (NMFS 2023a).

1.3 California Trout Petition to List Southern California Steelhead

On June 7, 2021, CalTrout submitted a Petition to the Commission to list Southern California steelhead, including both anadromous and freshwater resident life histories of *O. mykiss*, as endangered under CESA (CalTrout 2021). In their petition, CalTrout states their position as follows,

“CalTrout supports following the federal ESA listing coverage for below barrier steelhead, while keeping the above-barrier resident rainbow trout outside the ESA listing coverage.”

However, the CalTrout Petition deviates from the ESA listing by including freshwater resident fish below barriers within the listed steelhead distinct population segment (DPS).

On June 23, 2021, the petition to list Southern California steelhead under CESA was referred to CDFW for an evaluation of the scientific information presented therein and a recommendation whether to list, which was published in November 2021 (CDFW 2021). In their evaluation, CDFW (2021) notes that CalTrout (2021) defined Southern California steelhead as, “all *O. mykiss*, including anadromous and freshwater resident life histories, below manmade and natural complete barriers to anadromy” (CDFW 2021).

CDFW highlighted the fact that this proposed state designation differs from the ESA listing of a DPS of steelhead with the same geographic range that includes, “only naturally spawned anadromous *O. mykiss*,” (CDFW 2021), referring to NMFS’s 2006 listing of Southern California steelhead cited above. This deviation in the treatment of freshwater resident fish under the proposed state designation and existing federal designation raised uncertainty regarding the intent of the initial CalTrout Petition, which was resolved in a series of unpublished emails between CDFW and CalTrout in October 2021 confirming,

*“CalTrout defines Southern California steelhead as all *Oncorhynchus mykiss*, including anadromous and resident life histories, below manmade and natural complete barriers to anadromy... with the understanding that anadromous (adult southern steelhead) arise from anadromous and resident naturally spawning adults,” (as quoted in CDFW 2021).*

At the heart of this confusion between CalTrout—the listing organization—and CDFW—the regulatory agency tasked with providing the best scientific information to inform CESA listing by the Commission—is the issue of appropriate treatment of freshwater resident *O. mykiss* in an evaluation of sympatric (occupying the same geographic areas) anadromous *O. mykiss*. That keystone issue led to the development of the CFS LCM reviewed here, to address NMFS’s and CDFW’s lack of inclusion of the effects of freshwater life histories on anadromous Southern California steelhead population dynamics.

2 Review of California Department of Fish and Wildlife Status Report

2.1 Summary

2.1.1 Purpose and Context

CDFW's Status Review (CDFW 2024) evaluates whether there is sufficient scientific information to indicate that the continued existence of Southern SH/RT, throughout all or a significant portion of its range, is endangered or threatened. Although the federal ESA listing for the Southern California steelhead DPS includes only the anadromous life-history component, CDFW recommends the Commission list Southern SH/RT, which includes freshwater resident fish below barriers, under CESA. CDFW asserts legal authority to interpret what constitutes a species, justifying their departure from the federal listing.

2.1.2 Life History Considerations

Southern SH/RT enacts both freshwater and ocean migratory (anadromous) life history forms. The enacted life history depends on genetic factors, as well as environmental conditions such as freshwater rearing habitat availability, hydrologic conditions, and ocean access. CDFW provides evidence that the preservation of existing life history diversity within Southern SH/RT is important to foster long-term population stability, as this diversity provides a measure of redundancy that distributes risk, buffering populations from local extirpation or population-level extinction (collapse). They summarize their position regarding the importance of this life history diversity as follows:

"Ideally, all three Southern SH/RT life-history types (i.e., fluvial-anadromous, freshwater-resident, lagoon-anadromous) would be expressed within a single population, or the population would harbor the underlying genetic variation to express those life-history types when environmental conditions allow,"
(CDFW 2024, pg. 80).

CDFW states that, "it is unclear that the resident component can reliably produce anadromous fish after prolonged periods of unfavorable conditions in the long term."⁴ A recent viability assessment includes the statements of NMFS's understanding regarding the contributions of resident *O. mykiss* to steelhead populations:

- "We recognize that there may be situations where reproductive contributions from non-anadromous *O. mykiss* may mitigate short-term extinction risk for some steelhead DPSs," (NMFS 2023b, pg. 5).
- "Freshwater-resident (non-anadromous) forms of *O. mykiss* co-occur and appear to interbreed with the anadromous form in many populations, and new research has improved our understanding of the genetic architecture of the populations exhibiting both nonanadromous and anadromous forms (Pearse et al. 2014, Pearse et al. 2019). Thus, while not formally considered part of the DPS, resident

⁴ In support of this statement, CDFW cites "Boughton et al. 2022a," which is listed in their references as Boughton 2022. The Boughton or Boughton et al. 2022 document listed in the references of CDFW 2024 could not be located. It appears the correct citation for this statement is NMFS (2023): "Viability Assessment for Pacific Salmon and Steelhead Listed Under the Endangered Species Act: Southwest."

(nonanadromous) *O. mykiss* warrant consideration in managing for the anadromous life history” (NMFS 2023b, pg. 155).

- “To meet criteria for life-history expression, viable populations would need to consistently exhibit both the resident and anadromous life history, as well as a third life history of anadromous fish that rear in estuaries for a significant time prior to smolting,” (NMFS 2023b, pg. 176).

2.1.3 Life Histories Included in the Proposed Listing and Associated Assessments

CDFW states that,

“Non-anadromous resident O. mykiss... reside in many of these same streams and interbreed with anadromous adults, contributing to the overall abundance and resilience of the populations. Southern SH/RT as defined in the Petition include both anadromous (ocean-going) and resident (stream-dwelling) forms of O. mykiss below complete barriers to anadromy in these streams,” (CDFW 2024, pg. 139).

In fact, this proposition to include freshwater resident fish harkens back to NMFS’s initial position of including this life history within the listed DPS,⁵ which was retracted only after considering the substantial comments advocating against this approach, including comments from the U.S. Fish and Wildlife Service (FWS).⁶ Although the freshwater resident form is not considered in NMFS’s ESA listing, NMFS did include co-occurring freshwater resident *O. mykiss* in population assessments, where data were available. An expert panel of scientists from several federal agencies initially concluded the contribution of the freshwater resident life-history form to the viability of an *O. mykiss* ESU in-total is unknown and may not substantially reduce extinction risks to an ESU in-total (NMFS 2006). However, more recent science indicates that these resident life histories are likely to provide some mitigation to anadromous population viability, but the extent remains unquantified (NMFS 2023a).

2.1.4 Population Status and Trends

CDFW states that populations of freshwater resident and anadromous *O. mykiss* have both experienced drastic reductions in their abundances and ranges since the early 20th century, with declines in anadromous returns estimated to be over 90%. They further assert that available data indicate that populations of both the anadromous and nonmigratory life histories have remained critically low in the 21st century and have not recovered since listing under the ESA.

2.1.5 Departmental Position on Listing

Given the continued low abundances of freshwater resident and steelhead *O. mykiss* populations, CDFW believes consideration for CESA listing is justified. CDFW identifies multiple primary actions for protecting and restoring Southern SH/RT populations.

⁵ “While conclusive evidence does not yet exist regarding the relationship of resident and anadromous *O. mykiss*, NMFS believes available evidence suggests that resident rainbow trout should be included in listed steelhead ESUs in certain cases,” (NMFS 1997, pg. 43941).

⁶ “However, the FWS, which has ESA authority for resident fish, maintains that behavioral forms can be regarded as separate DPSs... and that absent evidence suggesting resident rainbow trout need ESA protection, the FWS concludes that only the anadromous forms of each ESU should be listed under the ESA,” (*ibid*).

2.2 Critical Evaluation of California Department of Fish and Wildlife Findings

The CDFW report provides an assessment of the status and trends of Southern California SH/RT, as well as the probable reasons for their decline and current obstacles to recovery. However, this assessment is based on limited data that may be incomplete and appear to have been inappropriately analyzed in certain cases. Moreover, while CDFW acknowledges interbreeding between sympatric populations of anadromous adult steelhead and freshwater resident rainbow trout, the populations are evaluated separately, with no accounting for the contributions of freshwater resident fish to steelhead population viability.

2.2.1 Data That Were Omitted from Analysis

Although a complete review of available data was beyond the scope of this evaluation, information provided by UCWD indicates that CDFW (2024) may have omitted important *O. mykiss* monitoring data from their assessment. For example, camera data from a diversion on the Santa Clara (Booth 2016) are mentioned by CDFW (2024) in Section 7.5.2 of their report (Other Monitoring Programs), but apparently not included in their analysis of steelhead population status and trends. Additional sources of data are mentioned in Section 7.5.2 of CDFW's report that appear not to have been incorporated into their status and trends analyses include snorkel surveys of fish abundance in the Santa Ynez River and video-based fish counts in the Ventura River.

2.2.2 Data That Were Inappropriately Analyzed

To paraphrase John G. Sheperd, Emeritus Professor at University of Southampton and former principal scientific adviser to the UK government on marine fisheries management, counting fish is like counting trees, except that you cannot see them and they keep moving around.⁷ Observed counts of a sample of animals or plants do not provide accurate estimates of population abundance unless they are statistically analyzed to account for the methods under which these data were collected (Cormack 1964; Jolly 1965; Seber and Le Cren 1967). Such treatment is needed to expand count data into an accurate estimate of population size. Abundance estimations derived from appropriate statistical treatment are less affected by the inevitable undercounting and double counting that occurs when counting individuals. Without this treatment, count data are observations that, at best, provide an index of total population abundance, but do not provide a robust estimate or quantify uncertain around that estimate.

However, count data from fish passage monitoring on the Santa Clara River (Booth 2016) are presented in CDFW's report as an estimate of *O. mykiss* abundance in the Santa Clara system. These observations of juvenile and adult *O. mykiss* presented in the Booth (2016) report have not been statistically analyzed to derive a robust estimate of overall population size (e.g., see Carlson et al. 1998; Macdonald and Smith 1980). Such analyses are required to account for trap efficiency, periods when gear was not operational, and differences in the overall level of effort associated with gear deployment.

After reviewing Section 4.2 (Sources of Information) in CDFW's report, it is not clear if any trap data or other fish enumeration data were treated statistically to develop the estimates of population size used in their Abundance and Trends Section (4.4).

⁷ The original quote is, "Managing fisheries is hard: it's like managing a forest, in which the trees are invisible and keep moving around," – John G Sheperd. Source: <https://jgshepherd.com/thoughts/>.

2.2.3 No Acknowledgment of Interbreeding

Within the CDFW (2024) report, abundance and trend data are presented separately for anadromous adults and “other” *O mykiss* (i.e., freshwater resident forms). Because of this separate treatment, the reproductive contributions of sympatric freshwater adult spawners to the production of smolts and future adult steelhead are not accounted for in measures of population status or the evaluation of long-term viability of Southern California steelhead.

Similarly, CDFW does not consider the potential contributions from above barrier populations of rainbow trout to the number of smolts resulting from downstream migration over barriers that can occur in some systems:

“The Department also considers Southern SH/RT to be markedly separate from above-barrier populations of O. mykiss in watersheds that are within the geographic scope of the proposed listing unit, because these above-barrier populations do not contribute substantially to the below-barrier populations of Southern SH/RT,”
(CDFW 2024, pg. 37).

A more specific definition of what CDFW considers to be an “impassable” barrier would enable a more thorough evaluation of CDFW’s approach. Depending on the level of contribution from above barrier populations to smolt production and anadromous adult spawners via downstream migration, these above barrier populations might also merit inclusion and protection under the CESA if they are measurably contributing to the anadromous populations.

3 Cramer Fish Sciences Life Cycle Model Technical Memorandum Review

3.1 Executive Summary

Cramer Fish Sciences (CFS) developed a technical memorandum in which they present a mathematical model (CFS LCM) for evaluating Southern California steelhead viability (CFS 2024). The CFS LCM was developed to address the California Department of Fish and Wildlife's lack of inclusion of the effects of freshwater resident life histories on anadromous Southern California steelhead population dynamics in their assessment of overall Southern California steelhead population viability, by accounting for freshwater resident contributions to the anadromous population. The model was constructed to accommodate variable environmental conditions and population demographics, enabling the exploratory evaluation of alternative scenarios.

3.1.1 Background

Within the petition to list under the California Endangered Species Act, Southern California steelhead is defined to include, "all *O. mykiss* below manmade and natural complete barriers to anadromy, including anadromous and resident life histories," from five biogeographical population groups.

The National Marine Fisheries Service (NMFS) has established a recovery goal for Southern California steelhead based on the number of adult anadromous spawners. NMFS acknowledges that freshwater resident trout and anadromous steelhead interbreed, but NMFS has not accounted for contributions to anadromous spawners from offspring of freshwater resident parents in the development of their recovery goal. Accounting for these contributions may change conclusions about population viability, as viability is assessed in relation to a recovery goal stated in terms of anadromous spawners.

To evaluate this possibility, CFS developed the CFS LCM, which is a "cohort-based life cycle simulation model" that includes both freshwater resident and anadromous life histories. The purpose of the CFS LCM is to simulate population dynamics (changes in abundance over time) and thereby evaluate extinction risk when freshwater life histories are available to contribute to anadromous populations.

3.1.2 Model Approach and Overview

The CFS LCM includes freshwater resident and anadromous populations and evaluates the effects of reproductive contributions from freshwater residents on the overall population viability of Southern California steelhead. The model has been initially parameterized using data compiled from a literature review and from a similar model developed by CFS for the Central California Coast steelhead DPS (the "Suisun Creek LCM").

The structure of the CFS LCM draws from the following simulation models developed for salmonids:

- NOAA's Habitat Restoration Planning (HARP) model (Jorgensen et al. 2021)
- The Shiraz model, developed collaboratively by researchers from NOAA, the University of Washington, Snohomish County Public Utility District, and the Tulalip Tribe (Scheuerell et al. 2006)
- CFS's Nooksack and Suisun Creek models

The CFS LCM simulates population dynamics over a modifiable time period (default of 125 years) for ten subpopulations of Southern California steelhead. The dynamics of all ten subpopulations are then aggregated to estimate overall Southern California steelhead DPS population dynamics.

The CFS LCM includes the following three life histories for each modeled subpopulation of Southern California steelhead:

1. Below-barrier anadromous populations
2. Below-barrier freshwater resident populations⁸
3. Above-barrier (perched) freshwater resident populations

The number of adults within each life history group are modeled separately, but the number of juveniles is modeled collectively for life history groups that are connected, with connection being based on environmental conditions. Offspring both from anadromous adults and from below-barrier freshwater resident adults always contribute to a collective pool of juveniles that either “smolt” in preparation for an anadromous life cycle or develop into freshwater resident adults (rainbow trout). Depending on the annual hydrologic regime (wet, average, or dry), offspring from perched freshwater resident adults may also contribute to this collective pool of juveniles that can smolt. Annual environmental conditions also affect juvenile survival and the proportion of below barrier juveniles that smolt. The CFS LCM follows cohorts of each life history group as they develop through distinct life stages (e.g., eggs, fry, smolts). The model accounts for survival associated with the transitions between these life stages and among the three modeled life history groups (Table 1). The default model settings for these transition rates are informed by empirical data that align with the current scientific understanding, but they can be adjusted individually by the user, for example, to simulate environmental scenarios.

Table 1. List of life stages and transitions included in the Cramer Fish Sciences life cycle model for Southern California steelhead

Life Stage or Transition Process	Description and Notes
Returns to Spawners	Determines the number of spawners for each life history group
Spawners to Eggs	Determines the number of eggs produced by adult females of each group
Egg to Fry	Determines the number of early-stage juvenile fish (fry)
Fry Rearing and Colonization (Survival)	An estimate of fry survival to the point of their initial winter
Winter Rearing Capacity and Survival	A density-dependent function for imposing fry mortality during winter
Summer Rearing Capacity and Survival	A density-dependent function for imposing parr mortality during summer
Smolt Rate	Rate that freshwater fish convert to anadromous life strategies.
Lagoon Rearing	Rate at which lagoon rearing occurs for smolts; alternative to estuary/ocean rearing
Estuary Survival	Rate at which anadromous smolts survive during estuary phase; default conditions for anadromous smolt rearing
Ocean Survival	Rate at which anadromous smolts survive during ocean phase; default conditions for anadromous smolt rearing
Maturation	Rate at which fish mature to spawners
Iteroparity	Rate at which spawners return and spawn again next year

⁸ CFS refers to this population as “Resident.”

3.1.3 *Impact of Environmental Conditions on Model Rates*

The model includes three types of annual hydrological conditions: wet, regular⁹, and dry. The reference condition is regular water availability, which is based on an average of historical records of the last 40 years of streamflow data.

During regular years, anadromous connection is maintained so that smolts can emigrate and anadromous adults can return to spawn. Perched populations do not contribute to below-barrier freshwater resident populations, and thus cannot contribute to anadromous populations through smolts.

During dry years, several adjustments are made to the regular year baseline. Perched and below-barrier freshwater resident populations experience reduced carrying capacity, smolt rate is reduced, and stray rate is increased. Perched populations do not contribute to below barrier freshwater populations.

During wet years, several adjustments are made to the regular year baseline. In wet years during which the perched freshwater resident population exceeds its carrying capacity, perched freshwater resident fish contribute to downstream (below-barrier) freshwater resident populations. These below-barrier freshwater residents can then contribute to the anadromous population by smolting.

The model also allows parameterization of a reduction event, which simulates a catastrophic die-off. This can be used to model a decrease in the number of spawners that can be applied for a set number of years to simulate drastic negative environmental impacts to the populations.

3.1.4 *Four Peaks' Assessment of the Value of the Cramer Fish Sciences Life Cycle Model*

When appropriately structured and parameterized, the CFS LCM will provide a tool for evaluating contributions from freshwater resident fish to the anadromous adult population. The model provides a logical mechanism for evaluating whether sympatric freshwater rainbow trout populations can support long-term viability of steelhead populations.

3.2 Critical Evaluation

3.2.1 *Model Summary*

The CFS LCM simulates transition rates among a set of model states to represent the transitions among various life stages of a developing fish (Table 2). The model simulates how eggs and parr mature and smolt to capture the interplay between anadromous and resident populations. Adults from the below-barrier freshwater resident group (referred to by CFS simply as the “Resident” group in the model framework and associated Shiny application) can contribute to anadromous adult returns, because all below barrier juveniles are “available” for smolting. Adults from the perched freshwater resident fish (referred to by CFS simply as the “Perched” group in the model framework and associated Shiny application) can contribute to below-barrier freshwater resident populations in wet years when the perched population density exceeds carrying capacity. The simulation-based framework allows users to account for uncertainty by entering different values for certain parameters (e.g., sequence of wet and dry years, survival rates).

⁹ CFS alternatively refers to average, medium, and normal environmental conditions. For the purposes of this evaluation, these three terms are assumed to refer to the same “Regular Years” condition described in CFS’s technical memorandum.

Table 2. Description of life stages and transitions included in the CFS LCM for Southern California steelhead

Life Stage or Transition Process	Description and Notes
Returns to Spawners	- Determines the number of spawners for each life history group - Estimated as the total number of spawners within each group, multiplied by pre-spawn mortality and harvest rates for that group - Parameterizable for each of the three life histories
Spawners to Eggs	- Determines the number of eggs produced by adult females of each group - Estimated as 50% of the total number of spawners (assuming half are female) times the fecundity value (the average number of eggs produced per female), which is parameterizable for each of the three life histories
Egg to Fry	- Determines the number of early-stage juvenile fish (fry) - Estimated by multiplying the number of eggs times the egg to fry survival parameter - Egg to fry survival is parameterizable for both above- and below-barrier freshwater populations
Fry Rearing and Colonization (Survival)	- An estimate of fry survival to the point of their initial winter - Estimated by multiplying the number of fry times the fry survival rate parameter - Separate estimates for perched and below barrier resident populations - Reduced in dry years
Winter Rearing Capacity and Survival	- A density-dependent function for imposing mortality during winter - This is parameterizable for each of the two freshwater life histories. - Uses a Beverton-Holt function (density dependent asymptotic function) so that incremental increases in rearing capacity/survival approach 0 as fry density increases - The Beverton-Holt function is dependent on habitat capacity and productivity, which differ among watersheds - This function assumes capacities by age account for effects of other age classes
Summer Rearing Capacity and Survival	- A density-dependent function for imposing mortality during summer - Otherwise, as above for Winter Rearing Capacity and Survival
Smolt Rate	- Rate that freshwater fish convert to anadromous life strategies - Each freshwater juvenile age class has an associated smolt rate that determines the proportion of that age class that will migrate to the ocean - Age and watershed dependent, only juveniles up to age 4 have the capacity to smolt, individuals older than this enact a fully freshwater life history
Lagoon Rearing	- Rate at which lagoon rearing occurs for smolts - Accounts for a strategy of anadromous smolts that provides greater survival for individuals rearing in lagoons compared to estuary and nearshore rearing - Density dependent function calculating amount of smolts that can rear in the lagoon, with the others being relegated to the estuary
Estuary Survival	- Default conditions for anadromous smolt rearing - Age specific survival rate times the number of estuary rearing smolts
Ocean Survival	- Default conditions for anadromous smolt rearing - Age-specific survival rate times the number of estuary rearing smolts
Maturation	- Rate at which fish mature to spawners - Separate rates for each life history group and age - Estimates of spawners within each life history group determined by multiplying age specific maturation rates times the number of fish in each age class for each life history and watershed - Also, anadromous spawners may stray to neighboring watersheds and contribute to the number of spawners via a straying rate
Iteroparity	- Rate at which spawners return and spawn again next year - Determines the number of adults that will repeat-spawn - Number of repeat spawners is calculated by multiplying number of spawners times the proportion of fish that respawn (iteroparity rate) and their probability of surviving spawning (respawn survival rate) - Assumes fish cannot change life histories once it is determined - Separate value for each life history

CFS has developed a reasonable and logically sound foundation for a cohort-based LCM to assess the role of environmental conditions and freshwater resident trout contributions on anadromous steelhead population dynamics. The CFS LCM was developed to address CDFW's lack of inclusion of the effects of freshwater life histories on anadromous Southern California steelhead population dynamics. If freshwater resident contributions to anadromous returns change population dynamics enough to affect viability, population recovery targets may benefit from a reevaluation. The modular nature of the cohort-based model provides a high degree of flexibility. Individual parameters can be used for different life stages, life histories, age classes, watersheds, and sub-watersheds. This means the CFS LCM can be used to evaluate knowledge gaps, test the effects of environmental and demographic conditions, and be updated as more information becomes available.

The CFS LCM is designed to evaluate relative differences in population outcomes as a consequence of changes to environmental or life history parameters relative to some baseline, providing guidance for future management and research actions. It is not designed to forecast accurate population abundances or develop recovery targets. However, it can be used to evaluate the assumptions used to determine recovery targets. While the basic model structure is adequate for examining Southern California steelhead population dynamics, key additions to the model structure are needed for the model to adequately address the questions posed by Association of California Water Agencies regarding current population abundance and the rate at which freshwater resident fish contribute to the anadromous population.

3.2.2 Strengths

- The CFS LCM is built on a flexible framework that incorporates relevant, recent, empirical data and information about Southern California steelhead.
- The CFS LCM includes components for resident and perched life history types, whose impacts were not included previously in CDFW's and NMFS's minimum viable population size assessments.
- The interactive GUI facilitates exploratory analyses and simple simulations.
- The model provides a framework for evaluating complex population dynamics that emerge from the interaction of freshwater resident, anadromous, and perched populations. The model incorporates effects of environmental variability, for example by modifying the contribution of perched fish and fry survival under different hydrologic conditions (i.e., "wet year" versus "dry year").
- Perched *O. mykiss* may contribute to below barrier populations and provide a buffering effect. Including a model structure with this phenomenon allows users to parameterize the magnitude of this effect based on professional opinion or emerging empirical data.
- Systematic simulations (e.g., sensitivity analyses) can be used to explore the ramifications of variance in these biological factors (see Section 4 for results from a set of these simulations).
- Other environmental factors that vary across years (e.g., ocean survival) are included in the model, but cannot be parameterized dynamically, to allow for differences among years.
- Systematic simulations can be used to explore the ramifications of variance in these environmental factors (see Section 4 for results from a set of these simulations).

3.2.3 Limitations

3.2.3.1 Summary of Limitations

While the current iteration of the CFS LCM uses sound logic and science, it does have several key flaws and limitations. One potentially important limitation of the model is that two key transition rates—the smolting rate and the ocean survival rate—are not life history specific. Offspring from anadromous parents and those from below-barrier freshwater resident parents are grouped together and share one set of transition rates between successive juvenile life stages (i.e., egg, fry, parr, smolt). While the framework accounts for contributions from freshwater resident adults to the number of returning anadromous adults, it does not support individually setting model parameters for these groups separately. This omission limits the range of simulations that can be analyzed and has implications for the accuracy of model output. Also, the fecundity rate for anadromous adults does not vary with age, to reflect the fact that older fish are larger and produce more eggs.

These flaws and other minor additional limitations are discussed in the following sections. These flaws and limitations should be addressed before the model is used in scientifically rigorous assessments of Southern California steelhead population dynamics and viability. However, upon incorporation of the revisions suggested below, the model would likely be an appropriate model of potential Southern California steelhead population dynamics.

3.2.3.2 Key Transition Rates Are Shared Between Life History Groups

The smolt rate is not individually parameterizable for offspring of each life history group. Smolt rate determines the relative occurrence of anadromy within the population being modeled, and thus the number of anadromous adult returns in the model's next step. In some ways, grouping all below-barrier juveniles is a strength of the model, as it considers all these fish to be freshwater residents, until they smolt. This approach enables a comprehensive Southern SH/RT viability assessment based on abundance of all juveniles, regardless of parentage. However, this identical treatment of all juveniles does not accurately reflect current scientific understanding.

Substantial evidence indicates that there are important genetic differences between populations of anadromous, below-barrier freshwater resident, and perched freshwater resident *O. mykiss*. A review of this evidence is presented in CDFW's recent Southern California steelhead Status Review (CDFW 2024). Key for this critical evaluation of the CFS LCM, the relative contributions to returning anadromous spawners differ among the different life histories, with anadromous spawners producing the highest proportion of future anadromous spawners (Abadía-Cardoso et al. 2019; Fraik et al. 2021). Thus, one set of smolt rates for all life histories is not appropriate in modeling the effects of these different life histories on anadromous steelhead abundance. The structure of the CFS LCM does not capture any reproductive isolation or reflect the genetic underpinnings of smoltification that may lead to different smolt rates between offspring of freshwater resident rainbow trout parents and those of steelhead parents.

The model also lacks the ability to set different rates of ocean survival for offspring of freshwater resident parents and those of anadromous parents. The size at which fish within a population smolt (size threshold) differs among life history groups, reflecting a heritable genetic component to smoltification (Phillis et al. 2016). Different size thresholds for smolting may translate into differences in size at ocean entry among smolts that originate from parents with different life histories. Size at ocean entry has been

shown to be affect marine growth rate—and, importantly, ocean survival—of smolts (Weitkamp 2015). Different ocean survival rates can contribute to differences in smolt-to-adult return ratios between life history groups, which would affect their respective ability to meaningfully contribute to returning adult steelhead abundance.

While this structure does not represent a “fatal flaw” in the CFS LCM, the model could be improved by including age-specific smolt rates for each life history, with a default parameterization that established offspring of anadromous fish having higher smolt rates than offspring of non-anadromous fish.

3.2.3.3 *Fecundity of Anadromous Adults Does Not Vary Among Ages*

The fecundity parameter within the model appears to be an average value (numbers of eggs) per female. All salmonids exhibit “size dependent fecundity,” meaning larger females produce more eggs (Fleming 1998), and *O. mykiss* are no exception (Jenkins et al. 2018; Schill et al. 2010). *O. mykiss* spawn at different ages and are capable of repeat-spawning over a range of ages, a process called kelting among steelhead that do so. Salmonids also exhibit “indeterminate growth,” meaning they continue to grow throughout their lifespan, and older fish are larger than younger fish (Mommensen 2001). Taken together this means that older *O. mykiss* are larger and produce more eggs than younger *O. mykiss*.

The range of size variation across age classes, and therefore fecundity, may not be very large in spawning female freshwater resident *O. mykiss* (Schill et al. 2010). However, the range in size at spawning for anadromous steelhead can be very large, leading to dramatic differences in fecundity (Jenkins et al. 2018). For example, adult steelhead kelts continue to grow after their first spawning, which has been shown to lead to an approximately 10% increase in fecundity between subsequent spawning events (Seamons and Quinn 2010). The CFS LCM could be improved by including an age-dependent fecundity parameter for all life history groups, especially the anadromous life history.

3.2.3.4 *Additional Considerations*

In addition to the model limitations described in Sections 3.2.3.2 and 3.2.3.3, the CFS technical memorandum could be improved by addressing the following concerns. These are less critical but addressing them would enable a more thorough evaluation of the mechanics of the model.

First, mathematical equations are not included in the memorandum or on the Shiny application. Equations should be included in all modeling efforts to enable evaluation of model assumptions. Similarly, the baseline parameterization of density dependent relationships is unclear. In several places (e.g., spawner to egg, winter rearing, summer rearing), baseline transition rates are unclear.

The choice of functional relationships and rationale for selection are not explained. Decisions regarding the type of functional relationships may be appropriate, but these are difficult to evaluate without an explanation of the rationale. Density dependent relationships can have strong effects on simulation trajectories. It is unclear why the “hockey stick” function is used to calculate egg production from spawners, but the Beverton-Holt function is used to calculate other metrics of density dependence such as winter rearing capacity and summer rearing capacity, and the lack of consistency was not explained.

Parameterization of Beverton-Holt and other density-dependent functions is not documented or described in the technical memorandum. These parameters of the density dependent relationships should be modifiable within the CFS LCM to best suit the system and population, as the level of density dependence could have a strong impact on simulation results. Additionally, the fry rearing calculations

do not appear to incorporate any density dependent dynamics. This is odd, because fry should also be subjected to similar density dependent phenomena as the other juvenile rearing populations. Further, while the lagoon rearing dynamics mention they are subject to density dependence, the memorandum does not indicate what mathematical function is being used (i.e., Beverton-Holt, hockey stick, or something else).

CFS's intention to publish the model in peer-reviewed scientific literature would provide an opportunity to subject the details of the model's structure, parameterization, and justification to a high level of scientific rigor. These details could also be included in an appendix to the Shiny application, but must be available somewhere, whether in peer-reviewed literature or the Shiny application for reference and evaluation.

3.3 Conclusions from Review of Life Cycle Model

Depending on contributions to anadromous spawning populations by below barrier freshwater resident populations and above barrier freshwater resident populations in wet years, the freshwater life histories may provide additional population stability and reduced extinction risk that should be accounted for when setting recovery targets. When appropriately structured and parameterized by addressing the aforementioned limitations, the CFS LCM will provide a tool for evaluating these contributions and determining whether sympatric freshwater rainbow trout populations support long-term viability of steelhead populations.

4 Cramer Fish Sciences Life Cycle Model Sensitivity Analysis for Southern California Steelhead

4.1 Sensitivity Analysis Introduction

Sensitivity analysis is a technique used to evaluate the performance of complex models and to understand the relative effect that individual model inputs or assumptions (parameters) exert on determining model outputs (predictions). In sensitivity analysis, critical parameters are identified and then varied systematically. The robustness of model predictions is evaluated by observing the change in model output that results from adjusting each parameter. Insights can be gleaned about the relative importance of each parameter by evaluating the range and distribution of outcomes.

In this way, the model's overall "sensitivity" to the value of individual parameters (sometimes referred to as parameterization, or parameter settings) can be evaluated, to identify the parameters that have the greatest effects on model results. The model is understood to be "sensitive" to the values of those parameters, which are thus considered important in determining the accuracy of model predictions. Those important parameters to which the model is highly sensitive then become a research priority to improve the accuracy of model predictions. This is particularly important for model parameters with high uncertainty. Highly uncertain parameters that strongly influence model results provide important caveats for model interpretation, and these should be prioritized when developing future research.

Four Peaks conducted a sensitivity analysis to test the influence of both basic model assumptions (robustness to starting population size) and uncertainty in important life history parameters including smolt rate, fecundity, and ocean survival. The following sections present a summary approach for the analyses, the results from these simulations, and finally a discussion of the implications of the findings. Of note, as it constitutes a point of departure from language used in the preceding sections, CFS's terminology regarding life history groups has been retained. Thus, in the subsections that follow, "Resident" refers specifically to the below-barrier freshwater resident group, while "Perched" refers to the above-barrier freshwater resident group.

4.1.1 General Approach

To evaluate the CFS LCM's sensitivity to individual parameters, a series of scenarios were constructed by systematically varying individual parameters while holding others constant. The parameters that were varied included initial abundance, fecundity, smolt rate, and ocean survival rate. This approach enabled an assessment of the differences in population trajectories under different values of that specific parameter.

Because the CFS LCM depends on the sequence of annual environmental conditions (wet, dry, or normal), Four Peaks ran all simulation scenarios under the following four different sets of environmental conditions:

1. All dry years
2. All normal years
3. Normal and dry (repeating sequence of normal, dry, dry, dry, normal)
4. Normal, wet, and dry (repeating sequence of normal, wet, dry, dry, normal)

These environmental conditions were chosen to represent potential proportions of wet, dry, and average moisture years. Table 3 presents a summary of the default conditions used for the eight model scenarios (varying initial abundance, varying fecundity, varying smolt rate, varying ocean survival).

Table 3. Default parameter values used in the eight model scenarios

Scenario	Life History	Initial Abundance (Number of Spawners)	Fecundity (Number of Eggs)	Smolt Rate	Ocean Survival
Default	Perched, resident, and anadromous	1,000 for all life histories	2,000 for anadromous populations 1,000 for freshwater populations	0.15, 0.5, 0.25, and 0.25 for ages 0 through 3 respectively	0.6, 0.36, 0.3, 0.3, 0.3, and 0.4 for ages 1 through 7 respectively
Vary starting abundance	All life histories simultaneously	0,500, 1000, 1500, 2000 for all life histories	Default Parameter Setting	Default Parameter Setting	Default Parameter Setting
Vary fecundity	All life histories simultaneously	Default Parameter Setting	0, 500, 1,000, 1,500, 2,000 for freshwater life histories 0, 1,000, 2,000, 3,000, 4,000 for anadromous life history	Default Parameter Setting	Default Parameter Setting
Vary fecundity	Resident/perched spawners only	1,000 for freshwater life histories, 0 for the anadromous life history	0, 500, 1,000, 1,500, 2,000 for freshwater life histories 0 for the anadromous life history	Default Parameter Setting	Default Parameter Setting
Vary fecundity	Anadromous spawners only	1,000 for anadromous life histories, 0 for the freshwater life history	0, 1,000, 2,000, 3,000, 4,000 for the anadromous life history 0 for freshwater life histories	Default Parameter Setting	Default Parameter Setting
Vary smolt rate	Resident/perched spawners only	1,000 for freshwater life histories, 0 for anadromous life history	1,000 for freshwater life histories 0 for anadromous life history	Defaults times factors of between 0 and 2	Default Parameter Setting
Vary smolt rate	Anadromous spawners only	1,000 for anadromous life history, 0 for freshwater life history	1,000 for anadromous life history 0 for freshwater life histories	Defaults times factors of between 0 and 2	Default Parameter Setting
Vary ocean survival	Resident/perched spawners only	1,000 for freshwater life histories, 0 for the anadromous life history	1,000 for the freshwater life histories 0 for the anadromous life history	Default Parameter Setting	Defaults times factors of between 0 and 2
Vary ocean survival	Anadromous spawners only	1,000 for anadromous life histories, 0 for the freshwater life history	2,000 for the anadromous life history 1,000 for the freshwater life histories	Default Parameter Setting	Defaults times factors of between 0 and 2

4.1.2 Vary Initial Abundance Simulations

A basic assumption of the CFS LCM is that the model's final population abundance estimates (and thus, the overall assessment of population viability) are robust to small differences in starting abundance. This assumption has implications regarding the importance of accurate estimates of current population size. To evaluate this assumption, Four Peaks ran scenarios that varied initial population abundances from the default of 1,000 spawners for each life history type by a factor from 0 to 2, in increments of 0.5 (e.g., [0, 1,000, 2,000, 3,000, 4,000] for anadromous spawners and [0, 500, 1,000, 1,500, 2,000] for freshwater spawners). The population trajectories for the 150-year time series were then averaged across all watersheds. Varying the initial population sizes was not expected to substantially affect model results because of the relative predictive nature of the model.

4.1.3 Vary Fecundity Simulations

Typically, age and life stage-structured models are sensitive to fecundity and other state transition rates. These parameters may also have the highest uncertainty. Simulations were constructed to evaluate variance in the fecundity parameter. Four Peaks ran scenarios that used the default initial population sizes for all life history groups, and varied fecundity estimates from the default of 1,000 eggs per spawner for resident fish and 2,000 eggs per spawner for anadromous fish, by a factor from 0 to 2, in increments of 0.5. The population trajectories for the 150-year time series were then averaged across all watersheds. Varying fecundity was expected to affect model results because fecundity has a direct impact on the number of progeny produced by spawners in each generation, which can affect the minimum number of spawners required to prevent population collapse (minimum viable population), a common recovery target that has been applied to Southern California steelhead.

4.1.4 Anadromous Contribution Simulations (Vary Smolt Rate and Vary Ocean Survival)

One of the major questions regarding the anadromous steelhead recovery target—quantified as the minimum viable population—is the degree to which resident and perched freshwater populations contribute to the anadromous spawning population. As discussed in Section 3.2.3.1, anadromous spawners have a higher probability than resident spawners of producing future returning anadromous adults. Two potential mechanisms of action for this have been identified: 1) a difference in smolt rates between the two life histories, or 2) a difference in ocean survival between the two life histories. Differences in smolting and other behavioral and physiological aspects of an anadromous life history are determined in part by genetics (Pearse et al. 2014). Survival after smolting is greater among larger sized smolts (Tatara et al. 2017), and anadromous parents generally give rise to larger offspring (Kendall et al. 2015). As currently formulated, the CFS LCM does not allow life history specific smolt rates (to specify a higher probability of smolting for offspring of anadromous parents) or ocean survival rates (to specify a higher probability of surviving in the ocean for offspring of anadromous parents).

To evaluate freshwater parent contributions to the anadromous population within the current structure of the CFS LCM, Four Peaks ran a scenario that set the anadromous starting population size and fecundity to 0, while maintaining the resident and perched starting population sizes and fecundities at the defaults (1,000 for both parameters). In this scenario, anadromous fish must arise from offspring of freshwater parents, so this tests the ability of the combined resident population to wholly support an anadromous population without any reproductive contributions from those anadromous adults.

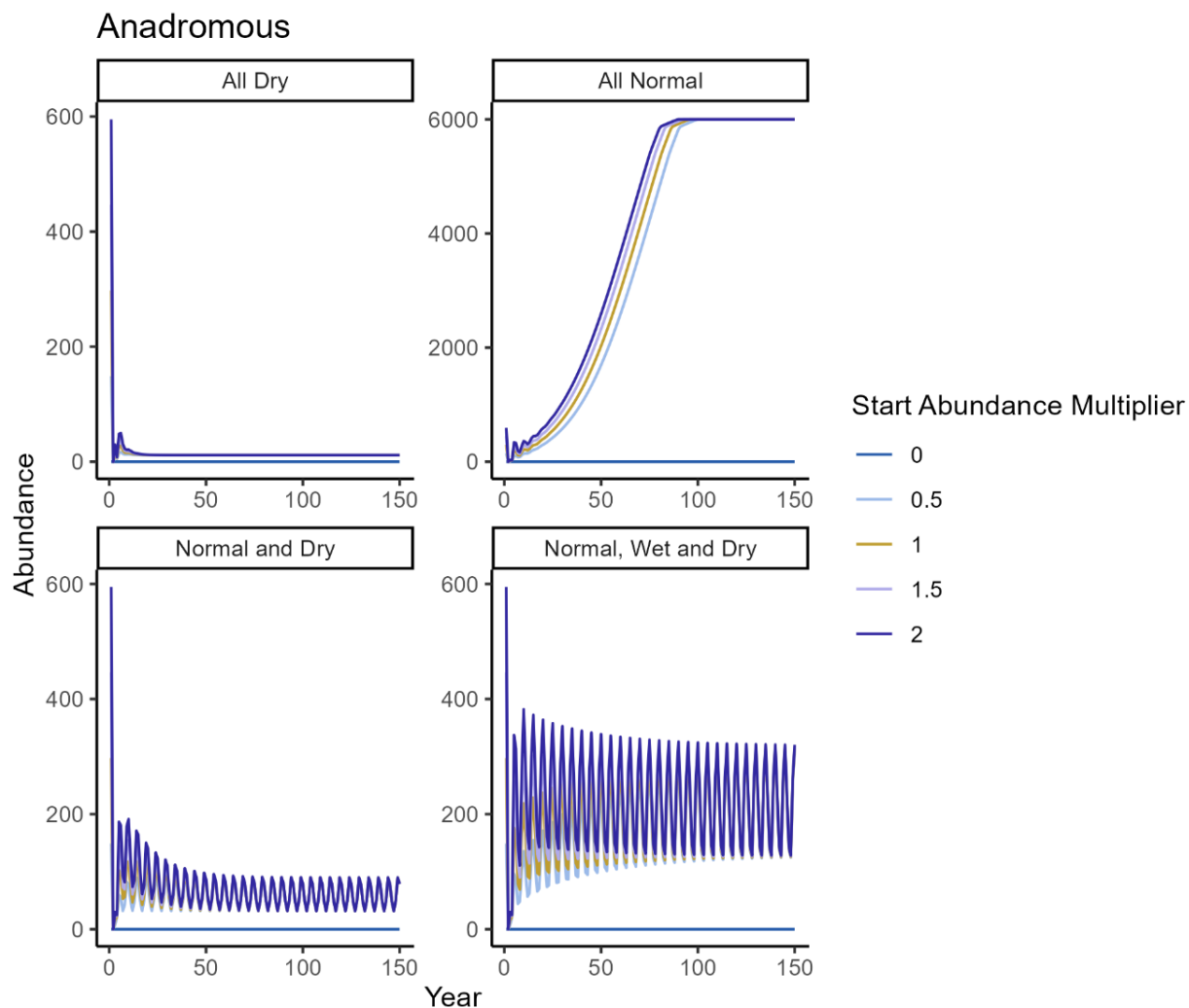
The converse of this scenario was also run, setting freshwater fecundities and starting populations at 0, the anadromous population fecundity at the default 2,000, and anadromous population size at the default 1,000. This scenario tests the ability of the anadromous population to support itself without any reproductive contributions from the resident adults.

Two sets of these scenarios were run: one that varied the smolt rate and one that varied ocean survival. These two parameter sets were varied from the default by factors between 0 and 2 with a step size of 0.5. Default smolt rates were 0.15, 0.5, 0.25, and 0.25 for ages 0 through 3, respectively. Default ocean survival rates from one age class to the next (starting at age 1 and ending at age 7) were 0.6, 0.36, 0.3, 0.3, 0.3, and 0.4, respectively. This allowed an assessment of the consequences of overestimation or underestimation of the unknown true parameter value.

4.2 Sensitivity Analysis Results

4.2.1 *Vary Starting Abundance Simulations*

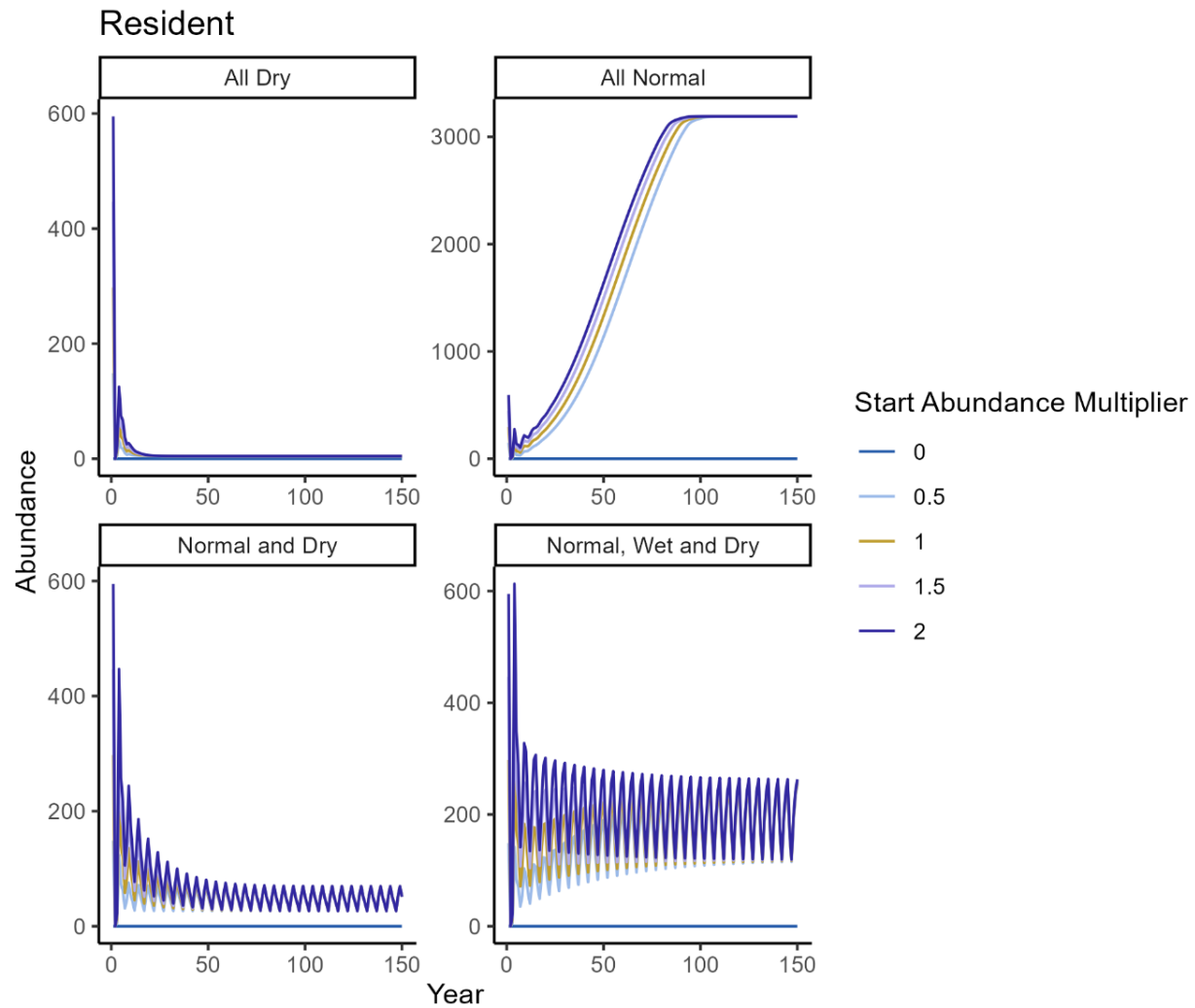
As expected, model results (i.e., ending abundance estimates and overall conclusions about population viability) were robust to starting population abundances (Figure 1 through Figure 3). Abundances towards the ends of the time series were similar among different starting abundances, provided the starting abundances were not extremely small. Only when wet years were included did the starting abundance make a noticeable but small difference in the average ending population abundances. Under scenarios with wet years and higher starting abundance, ending populations sizes were also slightly larger.



Notes:

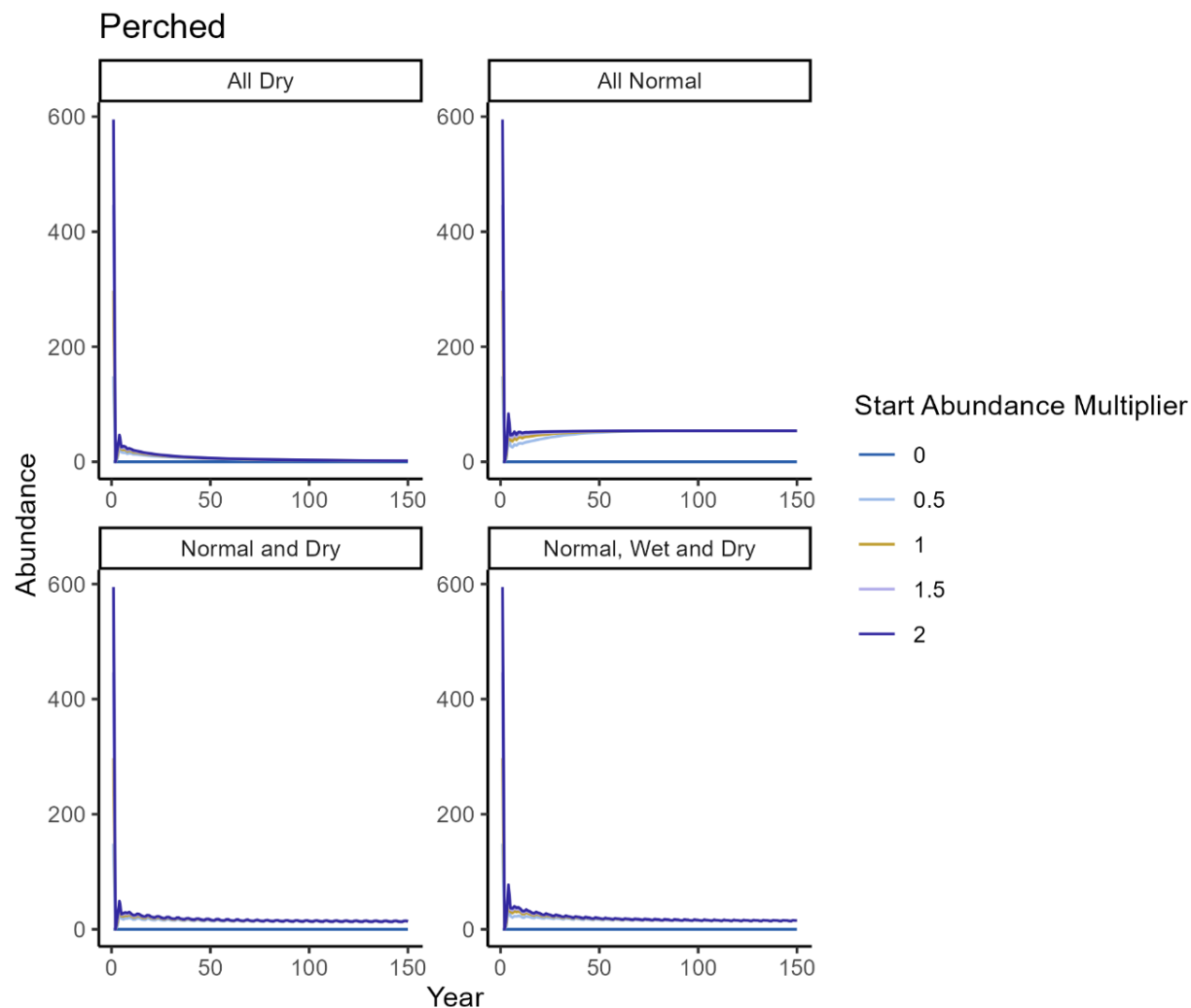
- Multiplier 0: Anadromous Start Abundance = 0, Resident and Perched Start Abundance = 0
- Multiplier 0.5: Anadromous Start Abundance = 500, Resident and Perched Start Abundance = 500
- Multiplier 1: Anadromous Start Abundance = 1000, Resident and Perched Start Abundance = 1000
- Multiplier 1.5: Anadromous Start Abundance = 1500, Resident and Perched Start Abundance = 1500
- Multiplier 2: Anadromous Start Abundance = 2000, Resident and Perched Start Abundance = 2000

Figure 1. Vary starting abundances, all life histories simulation: anadromous population trajectory using default fecundities of 1,000 eggs for resident and perched life histories and 2,000 eggs for anadromous life histories



Notes: See Figure 1 notes for multiplier ranges.

Figure 2. Vary starting abundances, all life histories simulation: resident population trajectory using default fecundities of 1,000 eggs for resident and perched life histories and 2,000 eggs for anadromous life histories



Notes: See Figure 1 notes for multiplier ranges.

Figure 3. Vary starting abundances, all life histories simulation: perched population trajectory using default fecundities of 1,000 eggs for resident and perched life histories and 2,000 eggs for anadromous life histories

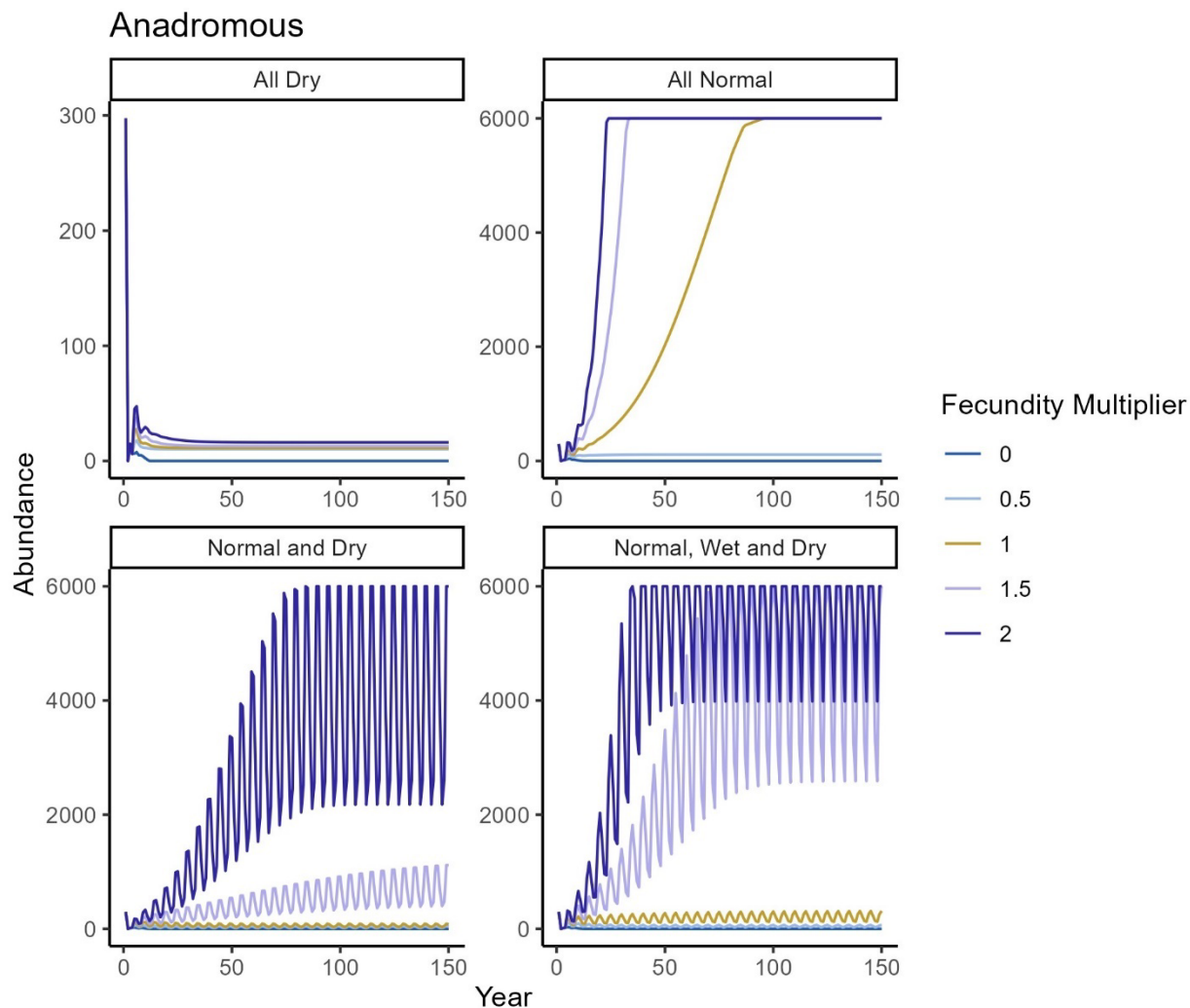
4.2.2 Vary Fecundity Simulations

4.2.2.1 Varying Fecundity for All Life History Groups

4.2.2.1.1 Effect on Anadromous Abundance

The effect of varying fecundity on model predicted ending abundance of anadromous adults depended on the environmental conditions of that model run (Figure 4). Under all dry conditions (top left panel in Figure 4), over- or under-estimation of the fecundity parameters for all three life histories had a relatively small impact on the model predicted average anadromous population abundance, because the model predicted average abundance is small regardless of fecundity. Under normal conditions (top right panel in Figure 4), overestimating the fecundity parameters increases the rate of population increase but has no impact on model predicted ending abundance, because abundance is limited by the carrying

capacity parameter. However, underestimating anadromous fecundity resulted in sharp reductions in model predicted ending abundance. Under normal and dry conditions (bottom left panel in Figure 4), if the default fecundity parameter estimate is an overestimate for each of the life history groups, it will have little impact because the model predicted ending abundances are already so low. However, if the current fecundity parameter estimate is below the true value, the model substantially underestimates the population abundance. Under normal, wet, and dry conditions (bottom right panel in Figure 4), if the current fecundity value is overestimated it will have little impact (populations are already very small), but if it is underestimated, the model may severely underpredict anadromous population abundances.



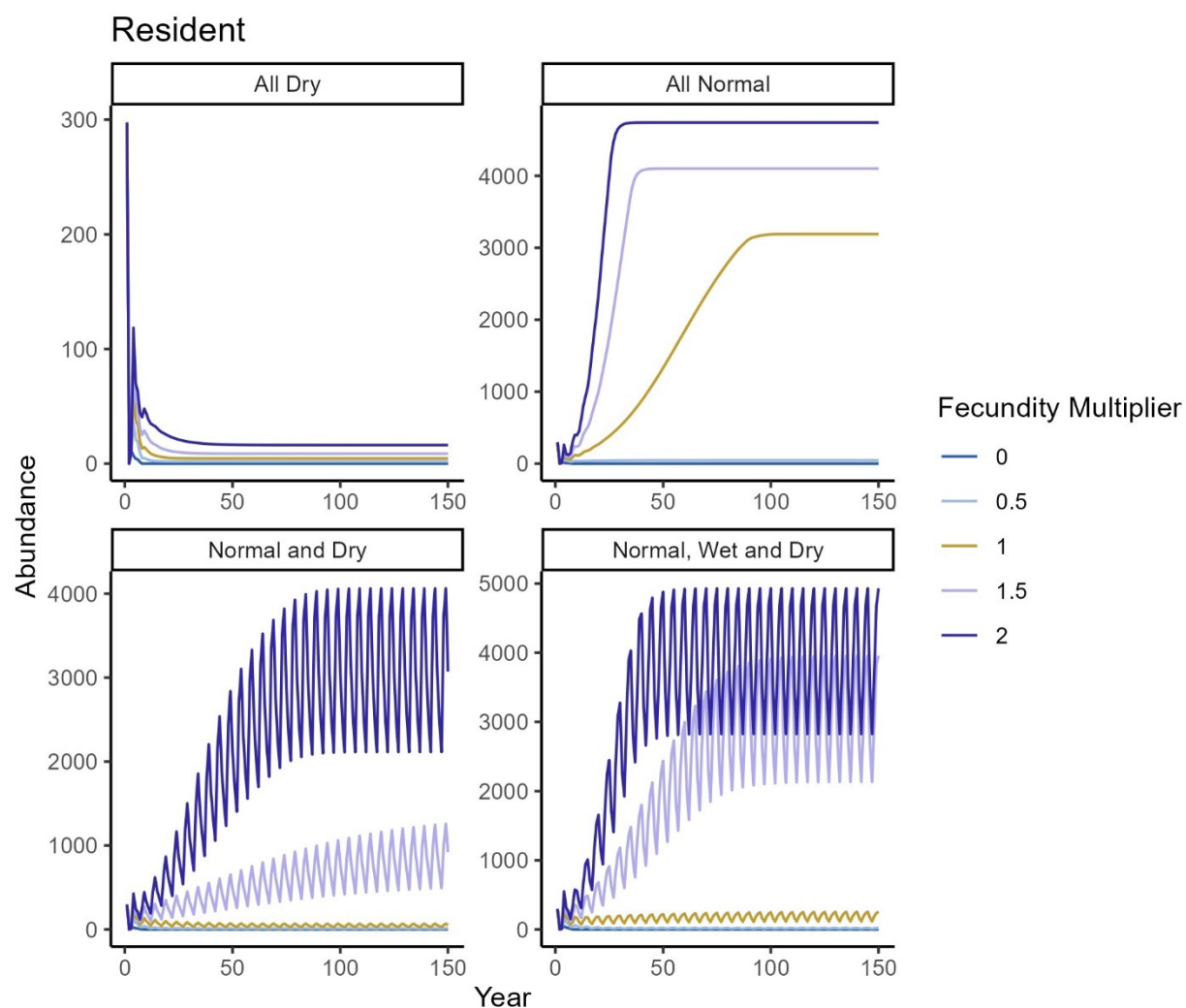
Notes: Starting population abundances were 1,000 for all life histories.

- Multiplier 0: Anadromous Fecundity = 0, Resident and Perched Fecundity = 0
- Multiplier 0.5: Anadromous Fecundity = 1000, Resident and Perched Fecundity = 500
- Multiplier 1: Anadromous Fecundity = 2000, Resident and Perched Fecundity = 1000
- Multiplier 1.5: Anadromous Fecundity = 3000, Resident and Perched Fecundity = 1500
- Multiplier 2: Anadromous Fecundity = 4000, Resident and Perched Fecundity = 2000

Figure 4. Vary Fecundity, all life histories simulation: anadromous population trajectory (averaged across watersheds) when varying fecundity for each life history group relative to the default of 2,000 for the anadromous population and 1,000 for the freshwater populations

4.2.2.1.2 Effect on Resident Abundance

The effect of varying fecundity on model predicted ending abundance of resident adults also depended on the environmental conditions of that model run (Figure 5). Under all dry conditions (top left panel in Figure 5), bias in the estimate of population fecundity would minimally impact model predicted ending freshwater population abundance. Under these conditions, extremely low population abundance reduces the potential variation in population abundance overall, and all scenarios result in near population collapse.



Notes: Starting population abundances were 1,000 for all life histories. See Figure 4 notes for multiplier ranges.

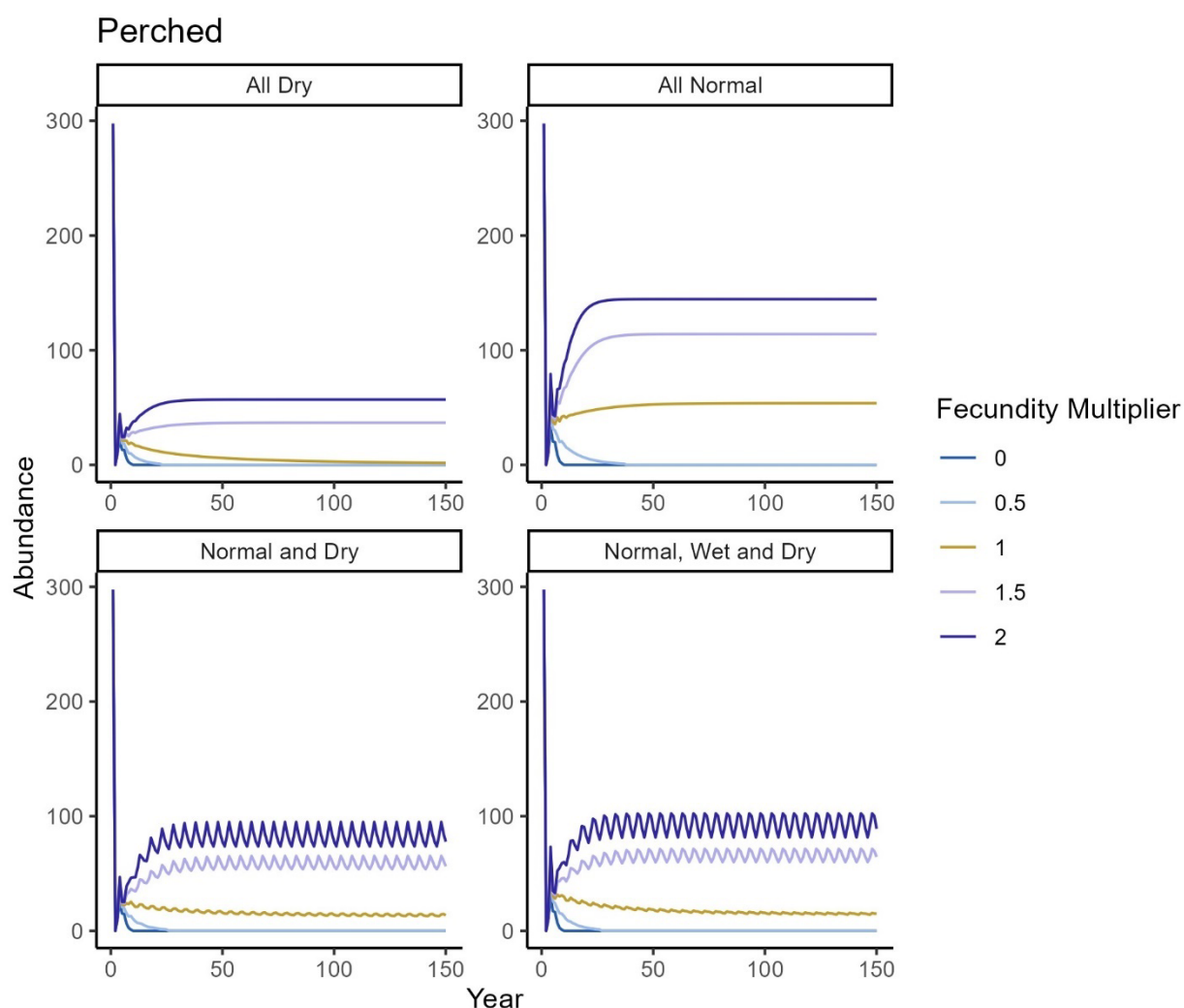
Figure 5. Vary fecundity, all life histories simulations: resident population trajectory (averaged across watersheds) when varying fecundity relative to the default of 1,000 for freshwater life histories and 2,000 for anadromous life histories

Under all normal conditions (top right panel in Figure 5), if current fecundity parameters are overestimated, the model would severely overestimate the model predicted ending population abundance. If the model's default fecundity is an underestimate, the model would only moderately underestimate the model predicted ending population abundance. Under normal and dry conditions (bottom left panel in Figure 5) or normal, wet, and dry conditions (bottom right panel in Figure 5), if the

current fecundity value is an overestimate it would have little impact, but if the current fecundity estimate is an underestimate the model could be drastically underestimating the model predicted ending abundance of the freshwater below barrier populations.

4.2.2.1.3 Effect on Perched Abundance

The effect of varying fecundity on model predicted ending abundance of perched adults was similar regardless of the environmental conditions of that model run (Figure 6). Generally, if the current perched fecundity is an underestimate, the impacts are more substantial on the average model predicted ending perched population abundance than if it is an overestimate. If the default perched population fecundity is overestimated, these populations are already relatively low, so the difference is small. If it is an underestimate, the model will underestimate the perched population size potentially substantially (though at a declining rate as the degree of underestimation increases).

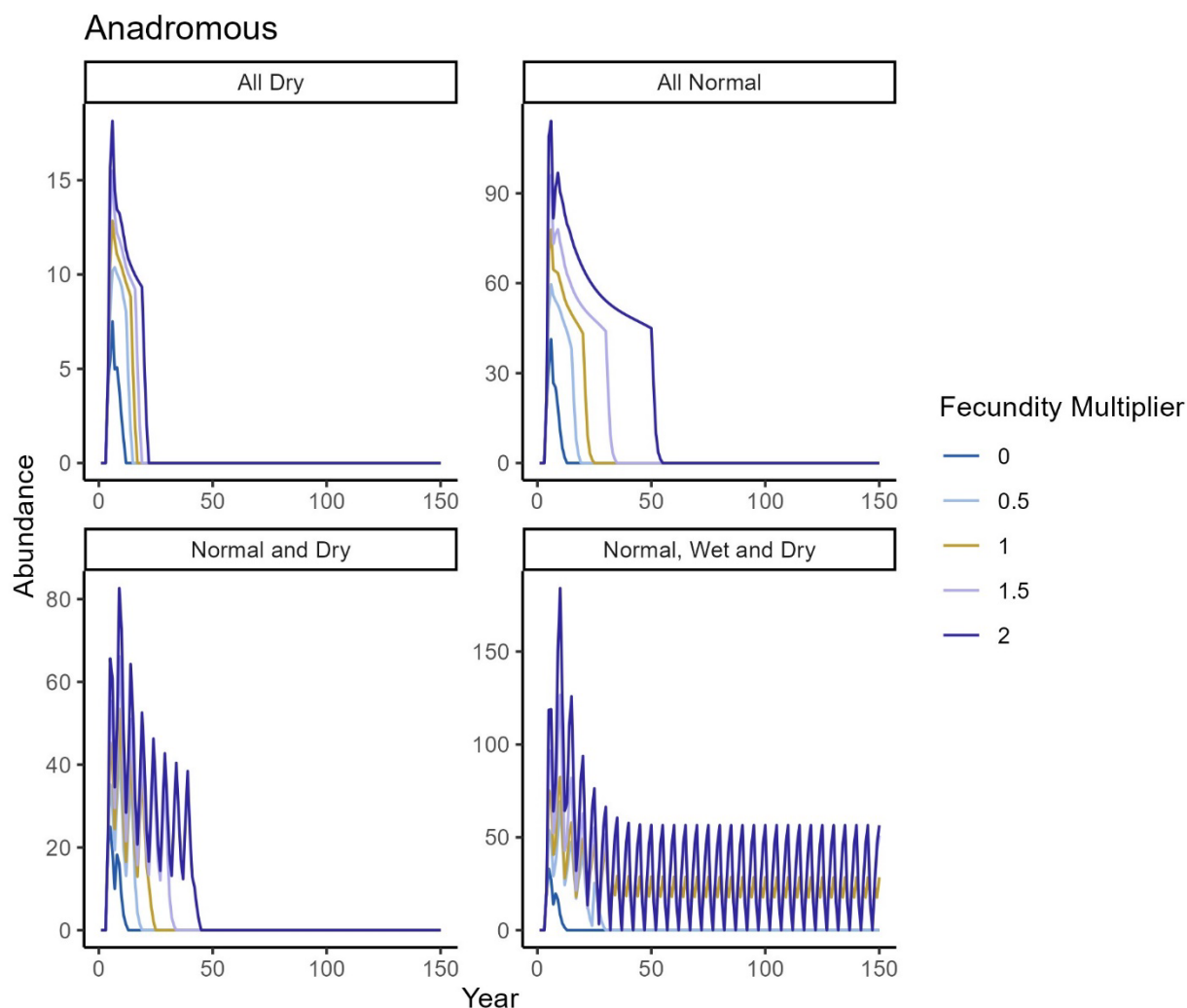


Note: Starting population abundances were 1,000 for all life histories. See Figure 4 notes for multiplier ranges.

Figure 6. Vary fecundity, all life histories simulations: perched population trajectories (averaged across watersheds) when varying fecundity relative to the default of 1,000 eggs for freshwater life histories and 2,000 eggs for anadromous life histories

4.2.2.2 Varying Fecundity for Resident and Perched Life History Groups Only

When anadromous adults are prevented from reproducing (i.e., fecundity is set to zero), under all dry, all normal, and normal and dry conditions, the anadromous population collapses (Figure 7). The freshwater populations are only capable of supporting the anadromous population when wet years are included, highlighting the importance of contributions from the perched population to downstream migrants in wet years (lower right panel in Figure 7). Even under these conditions, the model predicted average abundance is low at the end of the time series for the anadromous population.

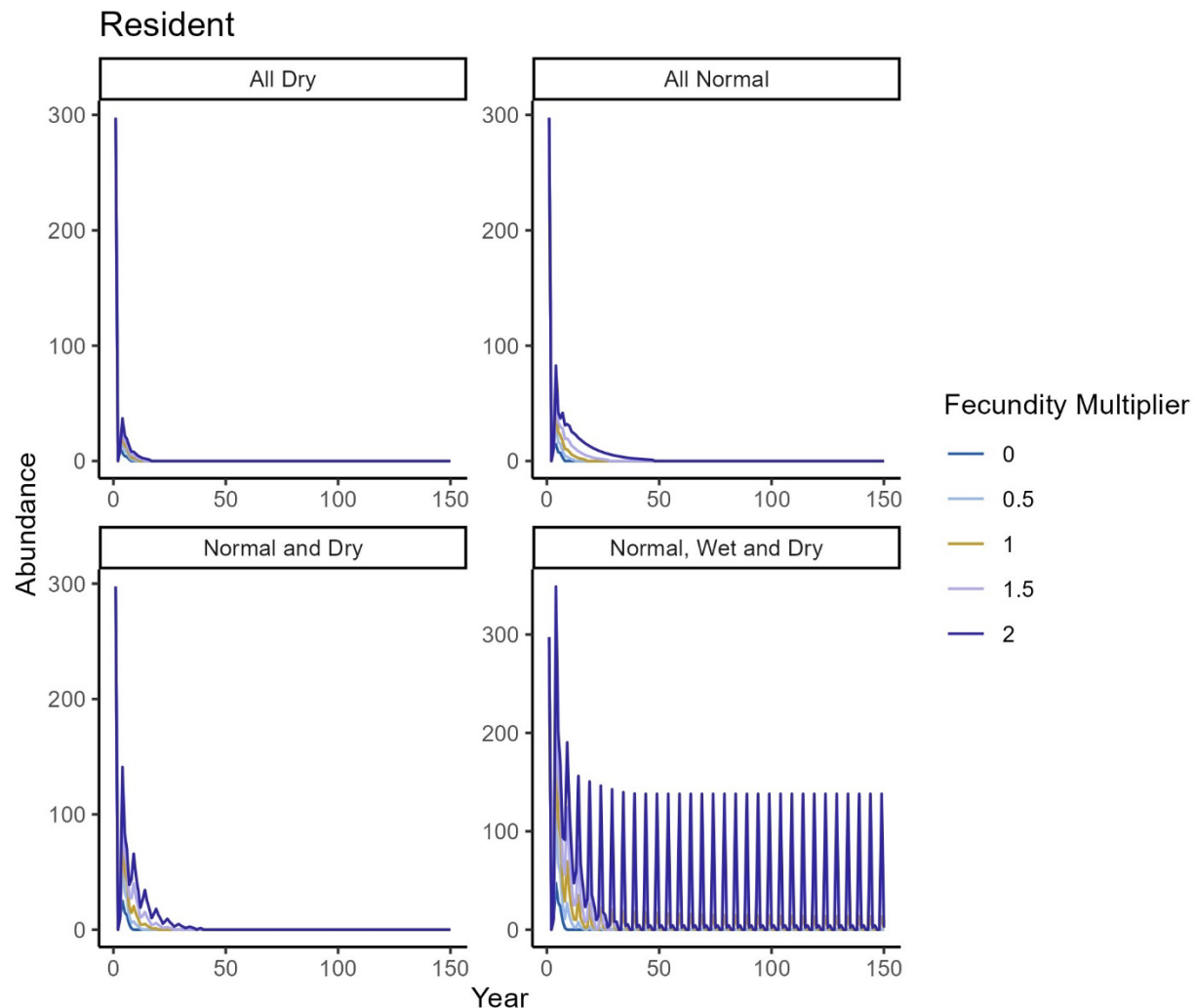


Notes: See Figure 4 notes for multiplier ranges.

Figure 7. Vary fecundity, resident and perched spawners only simulation: anadromous population trajectory (averaged across watersheds) when omitting anadromous fecundity contributions and varying perched and below barrier freshwater fecundity relative to the default of 1,000 for all populations

As the anadromous population declines, so too does the below barrier freshwater population (Figure 8), which eventually collapses unless wet years that allow support from the perched population are included (bottom right panel in Figure 8). This is an indicator that the below barrier freshwater and anadromous populations appear to be supporting each other. A collapse in one facilitates a collapse in

the other under climatic conditions that do not include wet years. Thus, only under the most optimistic conditions can freshwater populations maintain steelhead populations by themselves.



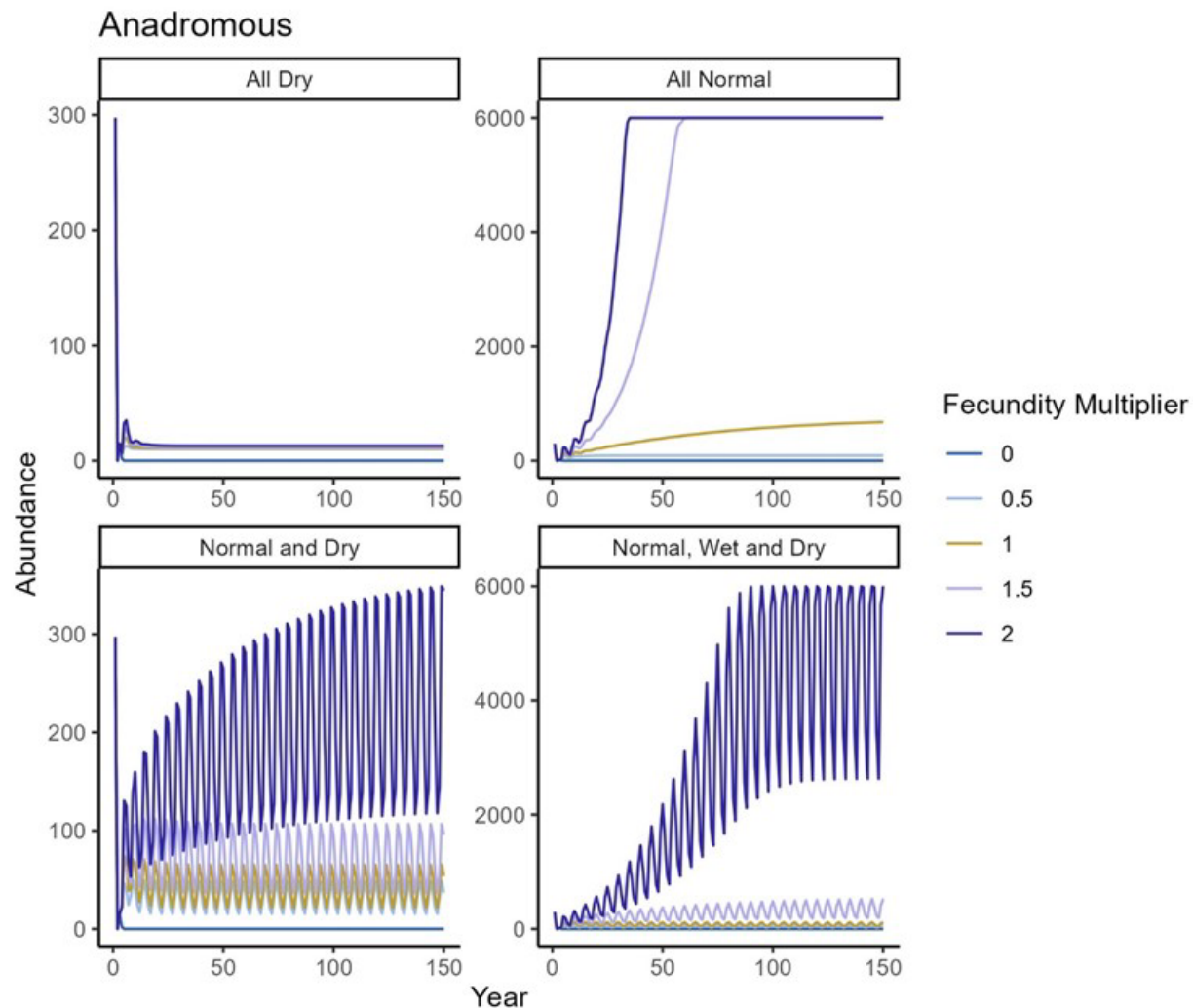
Notes:

- Multiplier 0: Anadromous Fecundity = 0, Resident and Perched Fecundity = 0
- Multiplier 0.5: Anadromous Fecundity = 0, Resident and Perched Fecundity = 500
- Multiplier 1: Anadromous Fecundity = 0, Resident and Perched Fecundity = 1000
- Multiplier 1.5: Anadromous Fecundity = 0, Resident and Perched Fecundity = 1500
- Multiplier 2: Anadromous Fecundity = 0, Resident and Perched Fecundity = 2000

Figure 8. Vary fecundity, resident and perched spawners only simulation: below barrier freshwater population trajectory (averaged across watersheds) when omitting anadromous fecundity contributions and varying perched and below barrier freshwater fecundity relative to the default of 1,000 for all populations

Varying Fecundity for Anadromous Life History Groups Only

Anadromous populations are capable of preventing their population's collapse without reproductive contributions from freshwater populations in all but the most adverse all dry scenario, but maintaining a robust population size required fecundity to be higher than the default model setting (Figure 9).



Notes:

- Multiplier 0: Anadromous Fecundity = 0, Resident and Perched Fecundity = 0
- Multiplier 0.5: Anadromous Fecundity = 1000, Resident and Perched Fecundity = 0
- Multiplier 1: Anadromous Fecundity = 2000, Resident and Perched Fecundity = 0
- Multiplier 1.5: Anadromous Fecundity = 3000, Resident and Perched Fecundity = 0
- Multiplier 2: Anadromous Fecundity = 4000, Resident and Perched Fecundity = 0

Figure 9. Vary fecundity, anadromous spawners only simulation: anadromous population trajectory (averaged across watersheds) when omitting resident and perched spawner fecundity contributions and varying anadromous fecundity relative to the default of 2,000 for all populations

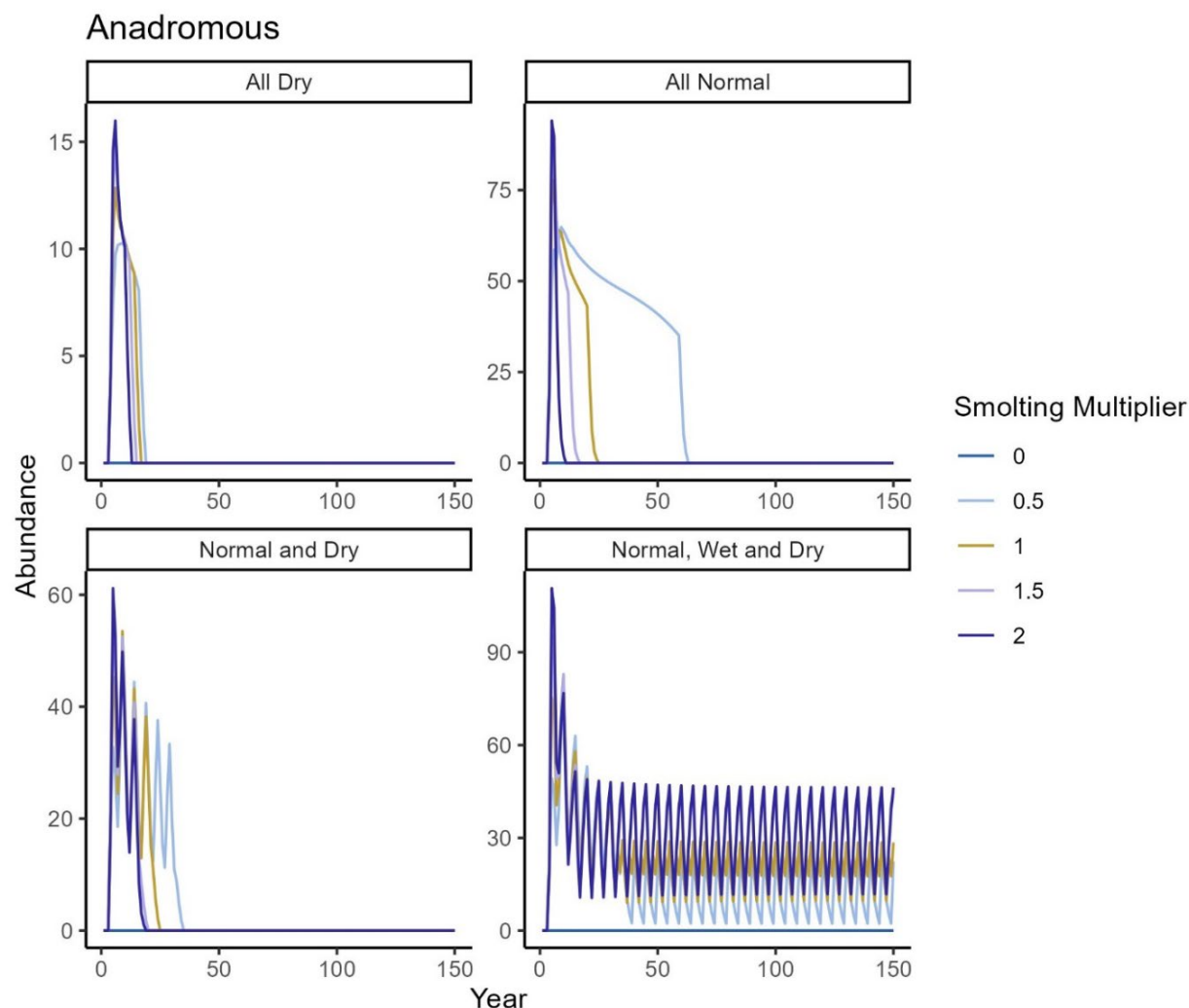
4.2.3 Anadromous Contribution Simulations (Vary Smolt Rate and Vary Ocean Survival)

4.2.3.1 Vary Smolt Rate

4.2.3.1.1 Resident and Perched Life History Groups Only

When anadromous fish starting population abundance and fecundity are set to 0, meaning all juvenile fish are offspring of resident adults, varying the smolt rate did not prevent the anadromous population from collapsing under all environmental conditions except the normal, wet, and dry conditions scenario

(Figure 10). Under these conditions, varying the smolt rate leads to a proportional difference in the model predicted ending abundance of anadromous adults. Regardless, even under these improbable future environmental conditions, the average anadromous population abundance is extremely low.



Notes:

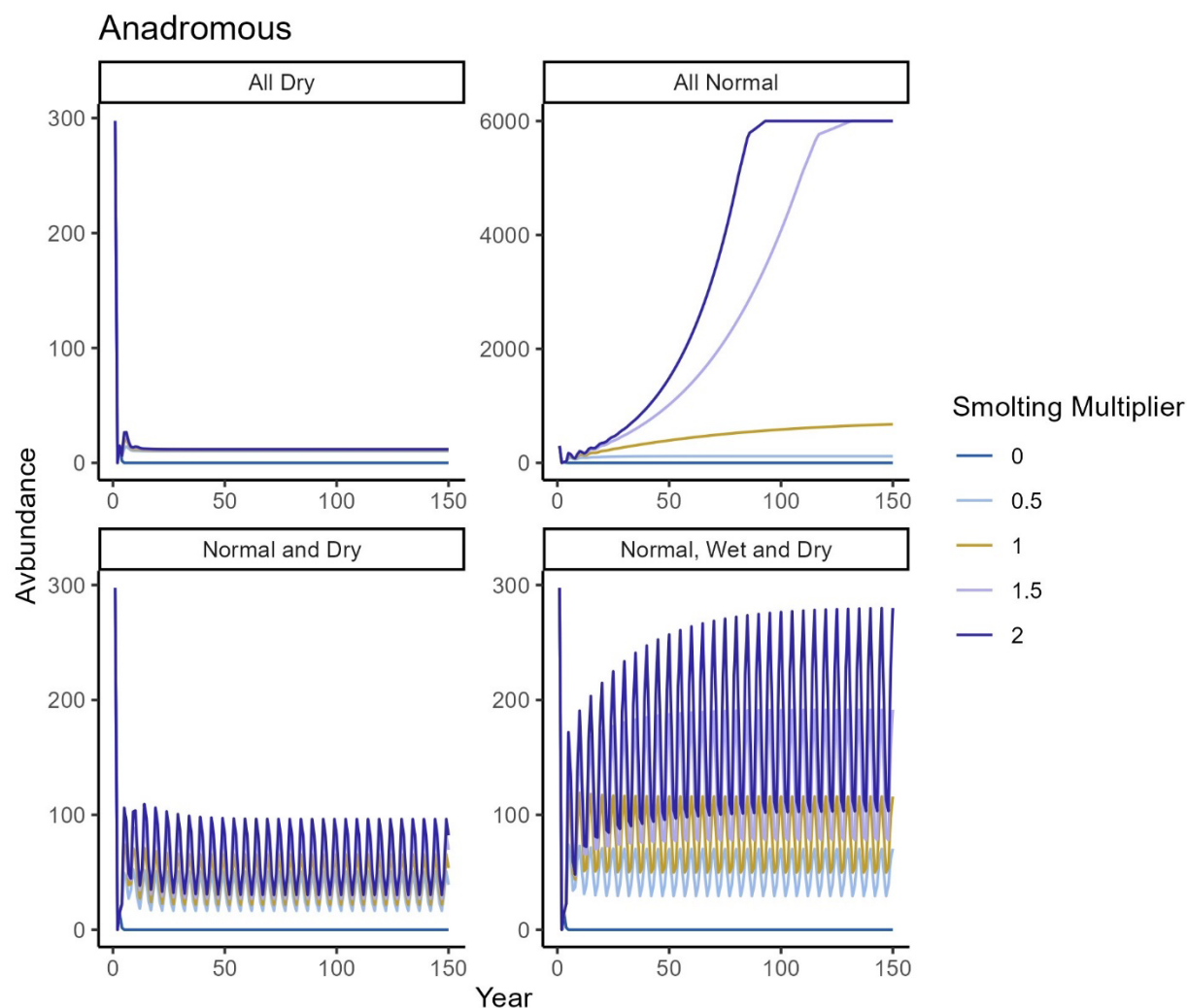
- Multiplier 0: Smolt Rates (Ages 0 through 3) = 0
- Multiplier 0.5: Smolt Rates (Ages 0 through 3) = 0.075, 0.250, 0.125, and 0.125
- Multiplier 1: Smolt Rates (Ages 0 through 3) = 0.15, 0.5, 0.25, and 0.25
- Multiplier 1.5: Smolt Rates (Ages 0 through 3) = 0.225, 0.750, 0.375, and 0.375
- Multiplier 2: Smolt Rates (Ages 0 through 3) = 0.3, 1.0, 0.5, and 0.5

Figure 10. Vary smolt rates, resident and perched spawners only simulation: anadromous population trajectory (averaged across watersheds) when omitting anadromous fecundity contributions and varying smolt rates relative to the defaults of 0.15, 0.5, 0.25, and 0.25 for ages 0 through 3

4.2.3.1.2 Anadromous Spawners Only

Conversely, the anadromous population can maintain itself and avoid collapse without reproductive contributions from freshwater spawners in most environmental conditions, depending on the rate of smolting (Figure 11). Based on current default smolting estimates, the anadromous population is able to

maintain itself in all tested environmental sequences except the all dry sequence (top left panel in Figure 11). If smolt rates are higher than the default estimate, they are able to maintain a small population even in all dry years. Under other environmental conditions, the model predicted ending abundance varies with smolt rate. This effect is greatest under all normal year conditions (top right panel in Figure 11) and least under normal and dry year conditions (bottom left panel in Figure 11).



Notes: See Figure 10 notes for multiplier ranges.

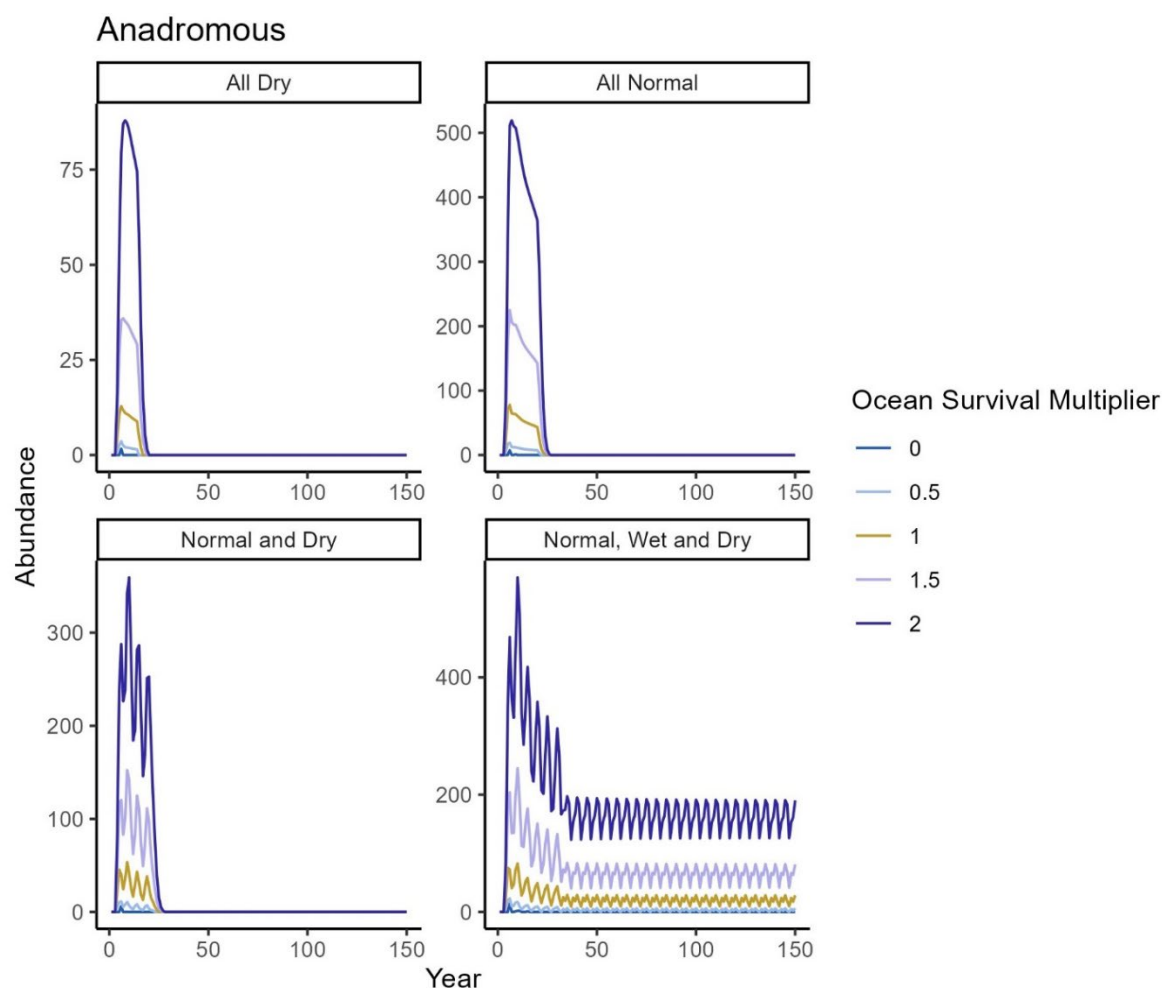
Figure 11. Vary smolt rates, anadromous spawners only simulation: anadromous population trajectory (averaged across watersheds) when omitting freshwater fecundity contributions and varying smolt rates relative to the defaults of 0.15, 0.5, 0.25, and 0.25 for ages 0 through 3

4.2.3.2 Vary Ocean Survival

4.2.3.2.1 Resident and Perched Life History Groups Only

When excluding anadromous reproductive contributions, and only freshwater perched and below barrier fish are allowed to contribute to the population, varying ocean survival had a substantial impact on model predicted ending anadromous abundance in years and under conditions when the population

did not collapse (Figure 12). However, the anadromous population collapsed within the first 25 years (essentially, during model burn-in) under all tested environmental conditions except under the normal, wet, and dry sequence (lower right panel in Figure 12). Under this scenario, if the current ocean survival estimate is an overestimate, the impact on model predicted average anadromous abundance is minimal because the population is already so low. However, if the current ocean survival parameter estimate is an underestimate, it would severely underestimate the true anadromous population abundance. This scenario of 1 in every 5 years being wetter than average is improbable when most climate change projections predict the drier environmental condition to become more common. Given that the resident and perched populations could not support an anadromous population under the less favorable drier scenarios (and even under all normal years), it is unlikely the resident and perched populations alone will be able to contribute meaningfully to anadromous spawner populations in the future.



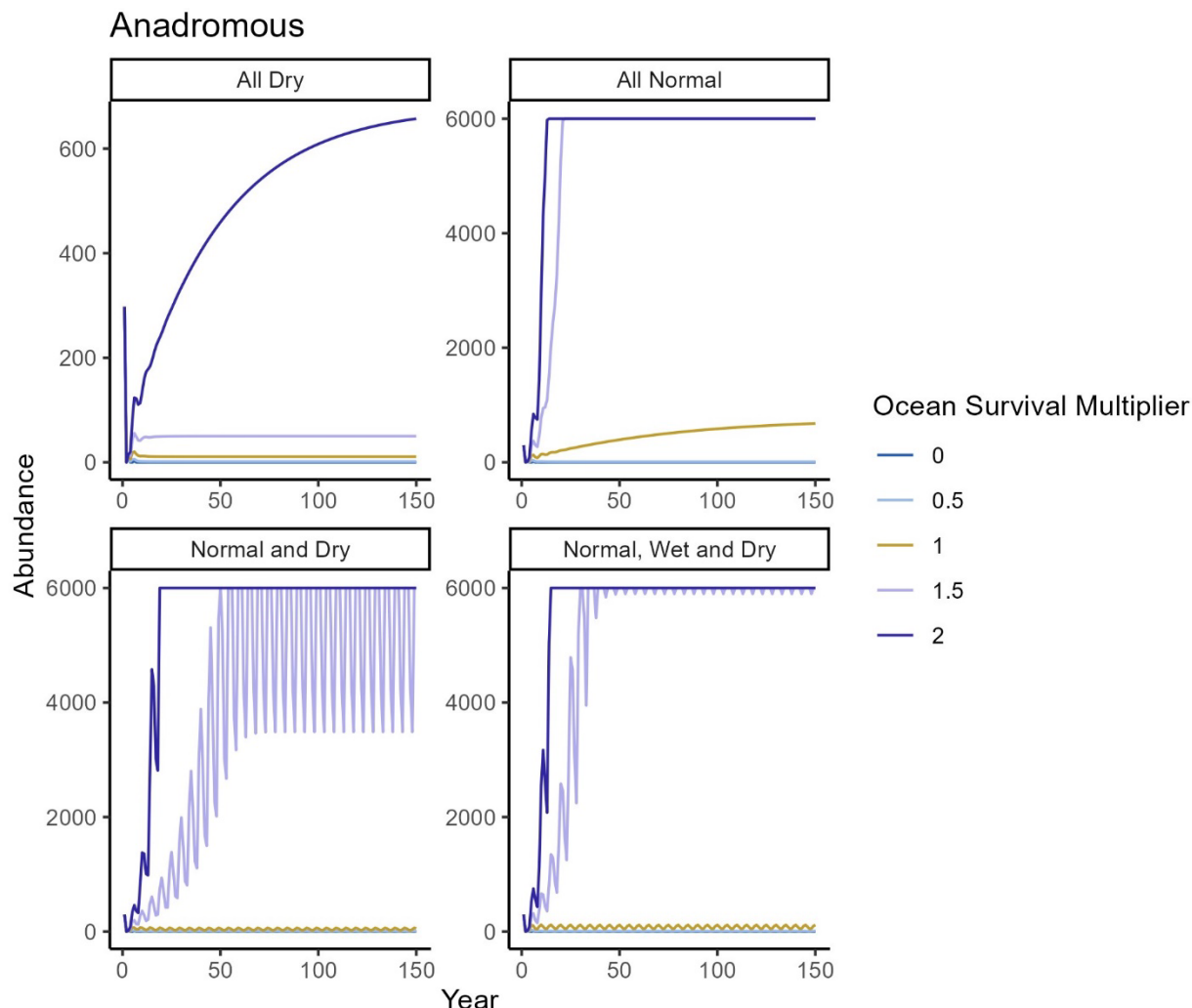
Notes:

- Multiplier 0: Smolt Rates (Ages 1 through 7) = 0
- Multiplier 0.5: Smolt Rates (Ages 1 through 7) = 0.30 0.18 0.15 0.15 0.15, and 0.20
- Multiplier 1: Smolt Rates (Ages 1 through 7) = 0.6, 0.36, 0.3, 0.3, 0.3, and 0.4
- Multiplier 1.5: Smolt Rates (Ages 1 through 7) = 0.90 0.54 0.45 0.45 0.45, and 0.60
- Multiplier 2: Smolt Rates (Ages 1 through 7) = 1.20 0.72 0.60 0.60 0.60, and 0.80

Figure 12. Vary ocean survival, resident and perched spawners only simulation: anadromous population trajectory (averaged across watersheds) when omitting anadromous fecundity contributions and varying ocean survival relative to the age specific defaults 0.6, 0.36, 0.3, 0.3, 0.3, and 0.4 for ages 1 through 7

4.2.3.2.2 Anadromous Spawners Only

Once again, the anadromous population can maintain itself without perched and resident reproductive contributions under all four tested environmental sequences depending on the ocean survival rate (Figure 13). However, under all environmental conditions, when ocean survival is at or below current default estimates, the population is frequently at or close to collapse without reproductive contributions from resident and perched spawners. Only if ocean survival rates are higher than the current default estimate, would anadromous populations alone be capable of supporting themselves without perched and resident reproductive contributions.



Notes: See Figure 12 notes for multiplier ranges.

Figure 13. Vary ocean survival, anadromous spawners only simulation: anadromous population trajectory (averaged across watersheds) when omitting resident and perched fecundity contributions and varying ocean survival relative to the age specific defaults 0.6, 0.36, 0.3, 0.3, 0.3, and 0.4 for ages 1 through 7

4.3 Conclusions from Model Sensitivity Analysis

- Importance of Starting Abundances
 - The CFS LCM is robust to starting abundances, provided they are not extremely small (less than 50% of default starting abundance estimates).
 - Populations fared better with more normal or wet years compared to more dry years.
- Importance of Fecundity
 - Model results are sensitive to fecundity estimates, particularly if fecundity is truly higher than the current default estimate.
 - If only resident and perched populations contribute to reproduction—even if the fecundity for these freshwater life history groups was set to be double the default model value—the anadromous population is predicted to collapse or to oscillate near collapse, and the freshwater life history groups also decline, due to less support from the alternate life history groups.
 - Only if anadromous fecundity was 50-100% greater than the default model estimate could anadromous spawning support a robust anadromous population without reproductive support from resident and perched spawners.
 - Model simulations lend support for the conclusion that maintaining robust populations of both anadromous steelhead and freshwater populations of both resident and perched fish will be important to maintaining viability of the anadromous life history.
 - Fecundity is an influential model parameter that is sensitive to parameterization
 - Four Peaks recommends that future model iterations prioritize accurate estimation of fecundity, particularly for anadromous spawners, to minimize uncertainty around this parameter; this may include age-specific fecundity rates that account for different numbers of year spent maturing in the ocean and kelting.
- Importance of Smolt Rates
 - If relying solely on resident contributions, the anadromous population persisted only in the presence of wet years with moderate to high smolt rates; even under these conditions, ending anadromous population abundances were still low.
 - However, under most environmental conditions, the anadromous population could sustain itself without reproductive support from resident and perched spawners, provided smolt rate is moderate to high.
 - Smolt rates were less influential than ocean survival rates on model predicted ending abundance.
- Importance of Ocean Survival
 - Resident and perched spawners alone (i.e., assuming no anadromous spawners) could support an anadromous population only under the improbable future scenario of high ocean survival and an environmental regime that included 1 of every 5 years being wetter than average.
 - Similarly, although anadromous spawners alone could support an anadromous population, under all conditions but the highest ocean survival scenarios, the model predicted ending anadromous population abundances were low if resident and perched spawners did not contribute to reproduction.

- Thus, high ocean survival could contribute to population viability regardless of the mixture of adult spawner life histories, but maintaining spawner populations of all life histories will provide the best chance of maintaining a robust population of the anadromous life history over the long term.
- Ocean survival was an influential parameter that is sensitive to parameterization.
- Four Peaks recommends that future research prioritize accurate estimation of age specific ocean survival to minimize uncertainty around this parameter, despite its difficulty.

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Appendix 2

Cramer Fish Sciences' Technical Memorandum

Southern California Steelhead Lifecycle Model

Draft technical memo on the lifecycle model developed by Cramer Fish Sciences for Association of California Water Agencies

Background

California Trout petitioned the California Fish and Game Commission (Commission) to list Southern California steelhead (*Oncorhynchus mykiss*; SCS) as endangered under the California Endangered Species Act (CESA). The petitioner defined SCS as all *O. mykiss*, including anadromous and resident life histories, below artificial and natural complete barriers to anadromy from the Santa Maria River, San Luis Obispo County (inclusive) to the United States-Mexico Border. The petition states that remaining SCS populations are in danger of extinction within the next 25-50 years. It also states that based on available abundance estimates, presence/absence data, and various threats within SCS range, populations appear extremely depressed or extirpated, and remaining populations are likely in immediate danger of extirpation. Therefore, the petitioner requested the Commission list SCS as endangered under the CESA. The Commission found that the petition contains sufficient scientific information to indicate action may be warranted.

The current National Oceanic and Atmospheric Administration (NOAA) National Marine Fisheries Service (NMFS) recovery population viability goal for SCS is 4,150 spawners per year on average, based on a “random walk with drift” model (Lindley 2003) and parameterized using Central Valley field data (Boughton et al. 2007; Williams et al. 2016). The NMFS report acknowledges interchange between the anadromous and resident populations, but does not include these effects in their viability goal. Viability studies recognize that genetic exchange between resident and anadromous groups would lower extinction risks of both groups and interchange between resident and anadromous forms could have consequences when determining extinction risk. In fact, the recovery plan for SCS (NMFS 2012) specifically states that recovery of the distinct population segment (DPS) will require “...protection, restoration, and maintenance of habitats of sufficient quantity, quality, and natural complexity throughout the SCS Recovery Planning Area so that the full range of all life history forms of *O. mykiss* (e.g., switching between resident and anadromous forms, timing and frequency of anadromous runs, and dispersal rates between watersheds) are able to successfully use a wide variety of habitats in order to overcome the natural challenges of a highly variable physical and biological environment.”

Therefore, it is important to assess if SCS extinction risk is sensitive to the details of the exchange between resident and anadromous life histories.

Model Purpose

The purpose of this work was to develop an adaptive lifecycle model that incorporates the proposed SCS listing population goals and allows for assessment of listing proposal

improvements to better protect and manage SCS into the future. We developed and enhanced this model to simulate various recovery goals, strategies, and what-if scenarios that also allow managers to manipulate specific portfolio parameters to understand how changes to key vital rates might influence population trajectories, under explicit model assumptions. Specifically, this model can be employed to understand how strengthening or weakening portfolios, including residency in the proposed goals, or inclusion of above barrier populations, influences the implied probability of future SCS extinction risk.

A goal of the Southern California steelhead life-cycle model (SCS LCM) is to better understand the influence of source-sink dynamics between resident and anadromous *O. mykiss* on population viability (i.e., the 100-year extinction risk) for Southern California DPS populations, as well as the potential for long-term Southern California DPS persistence as a whole. The model is meant to simulate various strategies including ratios of anadromy and residency, and various migration strategies that support each *O. mykiss* life stage along entire watershed corridors accessible to anadromous fish (including assumption of fish passage at artificial barriers). This exercise facilitates identification of key strategy alternative(s), and combinations thereof, and how they might best be implemented to support viable SCS population goals over various time periods (e.g., 20, 50, 100 years). To support this endeavor, this model was developed to simulate population trajectories under various SCS life history strategies (e.g., anadromy, residency, potamodromy, etc.), including management of a healthy SCS population into the future. This undertaking follows a general process for determining what combination of resident and anadromous strategies may support viable SCS population goals.

This lifecycle modeling effort incorporates well accepted modeling components to test key hypotheses and assumptions related to the proposed listing unit for SCS. It includes components of the Lindley (2003) and other models, such as the NOAA Habitat Assessment and Restoration Planning model (Jorgensen et al. 2021) or the Shiraz model (Scheuerell et al. 2006) which both rely on a multistage Beverton-Holt function to model production across the entire salmonid life cycle under a unified conceptual framework. In addition, the model is fully transparent, and is linked to well accepted functional relationships from population dynamics theory with the best available data to drive model outcomes. The model is also adaptable, so that as new data are available or outcomes from future hypotheses tests are received, they can be incorporated into the model. To facilitate collaborative stakeholder engagement in exploring model scenarios, we developed a user-friendly dashboard (or graphical user interface). By linking a state-of-the-science modeling framework with a user-friendly front-end, this effort provides a fully transparent, accessible modeling tool for assessing the conservation status of SCS and offers sound scientific guidance to discuss strategies and scenarios for future SCS population viability. This graphical user interface (GUI) provides a transparent tool with the ability to easily adjust parameters relevant to conservation.

Model Development Methods

Task 1: Gather and review background information

The goal of Task 1 was to gather and review background information relevant to the construction of a life cycle model (LCM) for Southern California steelhead (SCS). A literature search (e.g., Google Scholar, Web of Science) was used to identify, screen, and compile relevant biological information to inform and parameterize the life cycle model with empirical data where available. The following keywords were used to conduct the initial literature search:

Steelhead **OR** *Oncorhynchus mykiss* **OR** *O. mykiss* **OR** Rainbow trout
AND California **OR** Southern California **OR** Santa Maria **OR** Santa Ynez **OR** Santa Clara **OR**
San Gabriel **OR** Santa Ana **OR** San Luis Rey **OR** San Diego **OR** Piru Creek **OR** Sisquoc River
OR Cuyama River **OR** Ventura River **OR** San Mateo Creek **OR** Los Angeles River

AND Egg **OR** egg-to-fry **OR** larval **OR** emergent fry **OR** fry **OR** parr **OR** smolt **OR** adult **OR**
spawning **OR** spawner **OR** half-pounder **OR** resident **OR** resident life history **OR** life
history

AND freshwater **OR** delta-bay **OR** delta **OR** estuary **OR** lagoon **OR** ocean **OR** marine

AND survival **OR** mortality **OR** smolt-to-adult ratio **OR** SAR **OR** escapement
AND Reproduction **OR** fecundity **OR** fertility **OR** spawning success **OR** eggs **OR** stock-
recruit **OR** redd **OR** redd size **OR** redd distribution **OR** recruits per spawner **OR** spawners
per recruit

AND iteroparity **OR** iteroparous **OR** semelparity **OR** semelparous

AND Migration **OR** immigration **OR** emigration **OR** straying **OR** residency

AND Rate **OR** speed **OR** proportion **OR** probability

AND temperature **OR** drought **OR** flow **OR** instream flow **OR** El Niño **OR** La Niña **OR**
Pacific Decadal Oscillation **OR** PDO **OR** North Pacific Gyre Oscillation **OR** NPGO **OR**
upwelling **OR** sea surface temperature **OR** SST

Objective 1.1 Quantify minimum viable steelhead population

Source-sink dynamics is an established ecological theory which describes how dispersal between habitats of variable quality and connectivity can explain patterns in population viability and persistence (i.e., long-term viability) over large spatial or temporal scales (Pulliam 1988; Dias 1996). In source-sink theory, population viability can be maintained via the exchange of organisms between geographically separate meta-populations in a network of “source” populations (exhibiting positive population growth rates), and “sink” populations (exhibiting

negative population growth rates). Habitat fragmentation, in part due to installation of dams and diversions, has blocked upstream migration in much of Southern California and has geographically divided *O. mykiss* spawning populations by life-history types (Boughton et al. 2015; Fejtek 2017; Abadía-Cardosa et al. 2016). Non-anadromous *O. mykiss* frequently co-occur with anadromous *O. mykiss* within the same watersheds in Southern California and can co-occur within the same below-barrier stream reaches, but are often geographically separated where fish passage barriers block migration, thus forming potential source (above barrier) and sink (below barrier) populations. Genetic analyses of microsatellite data have concluded that geographically separated *O. mykiss* populations within the same watersheds (above and below barriers) are closer relatives than populations between watersheds (Clemento et al. 2009; Leitwein et al. 2017). Closer genetic distance and potential for population spillover implies that resident populations above barriers could mediate population viability and long-term persistence.

A viable individual population is defined in the 2012 Southern California Steelhead Recovery Plan (hereafter; the SCS Recovery Plan) as having less than a 5% risk of extinction due to threats from demographic, environmental, and genetic variation over the next 100 years (NMFS 2012). Similarly, a viable distinct population segment (DPS) is defined by a sufficient number of **spatially dispersed, yet genetically connected** populations to maintain long-term (1000+ years) persistence and evolutionary potential (McElhany et al. 2000; NMFS 2012). A “random-walk-with-drift” model was used in the SCS Recovery Plan to determine population-level biological recovery criteria based on a minimum viable population (MVP) size of individual populations for SCS steelhead, as well as DPS-level recovery criteria based on viable individual minimum populations within each Biogeographic Population Group, and other considerations (Lindley 2003; Boughton et al. 2007; NMFS 2012). This approach recommended an MVP of 4,150 annual anadromous spawners, on average, for an individual population. However, the approach assumed no empirical data were available for specific local populations, thus it is highly generalized and may not be well suited for every watershed (Boughton et al. 2007). A NMFS (2016) report also proposes using a 20-year window to evaluate the population, as opposed to simple annual check (Figure 1). Further, due to a lack of data on life history polymorphism and inability to estimate the magnitude of a “rescue effect” between resident and anadromous populations, the prescriptive criteria assumed that such a rescue effect is negligible; a 100 percent anadromous fraction was required of the mean annual run size criterion, and resident spawner life history variants (i.e., Rainbow Trout) were not considered in the MVP size criteria developed by NMFS (Boughton et al. 2007).

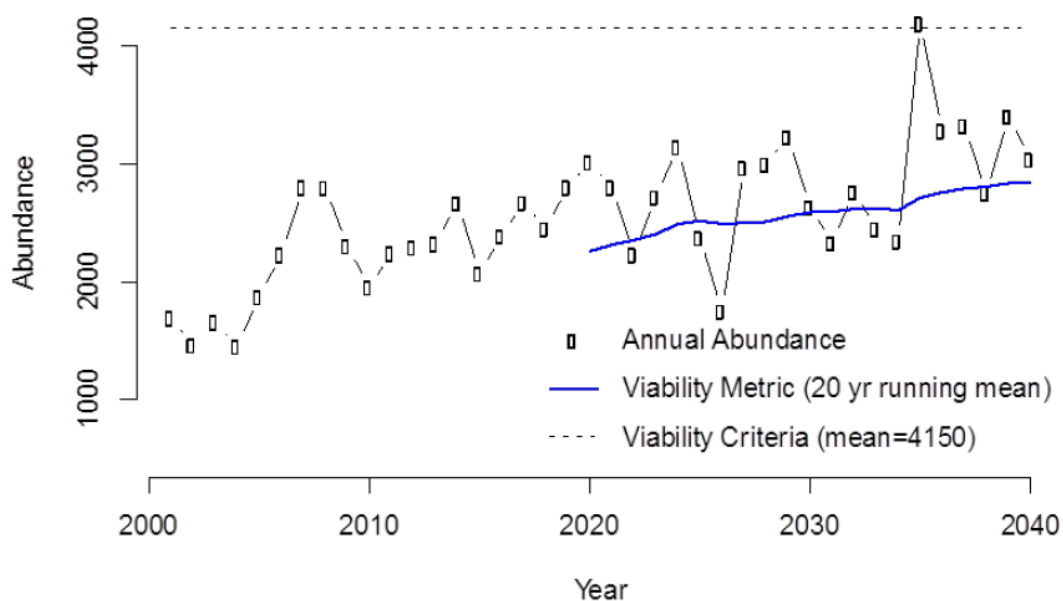


Figure 1. Concept of viability metric and a viability criterion applied to a hypothetical population. Figure 2 in NMFS 2016.

Objective 1.2 Identify population goals and dispersal amongst key watersheds

There is limited data to speak to potential and historical population demographics of steelhead in each watershed and basin. The literature has provided wide variations in estimated contributions to the population between basins. For example, Titus et al. (2002) estimated historical capacity of 20,000 for the Santa Ynez, but only 4,000 for the Ventura. Henke (1994) proposed between 7,000—9,000 for the Santa Clara, while Clanton and Jarvis (1946) only estimated 2,000—2,500 for the Matilija. Similarly, we have observed that smolt rates differ between basins, which again emphasizes the need to model the resident life history simultaneously to the anadromous population (Sogard et al. 2012). Although the SCS population is currently thought to be under capacity, these estimates help us determine the potential watershed population goals, the allocations that could contribute to the spawners needed for a MVP, if 4,150 anadromous spawners are appropriate and how resident spawners should be accounted for (e.g., less than a 100 percent anadromous fraction recovery criterion).

Objective 1.3 Southern California steelhead life history

Cramer Fish Sciences previously compiled data on 92 steelhead population parameters across 10 categories from 23 unique sources for the Suisun Creek LCM (Central California Coast DPS). Where data and parameter estimates from the Southern California DPS were not available, we used the information compiled for the Suisun Creek LCM to help inform parameterization. The following information on life histories, periodicity, and other demographic parameters from the literature review were completed as part of this project.

Migration and Spawning

Migration and spawn timing data from the Mokelumne River (California Central Valley DPS) shows entry into freshwater beginning in October and extending through April the following year, and spawning ranging from December to April (Figure 2) (East Bay Municipal Utility District, unpublished data).

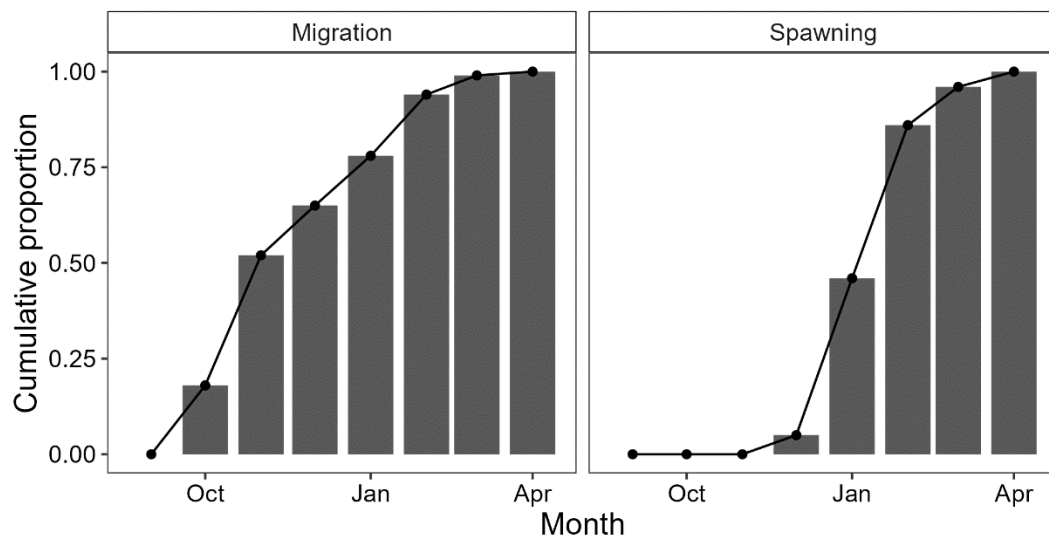


Figure 2. Cumulative proportion curves for migrating and spawning steelhead adults from the Mokelumne River (East Bay Municipal Utility District, unpublished data).

We assumed a 1:1 spawner sex ratio (Shapovalov and Taft 1954). Egg deposition assumes an average of 1,000 eggs per female, an optimistic estimate determined through a power-law relationship with fork length (Figure 3) (Shapovalov and Taft 1954).

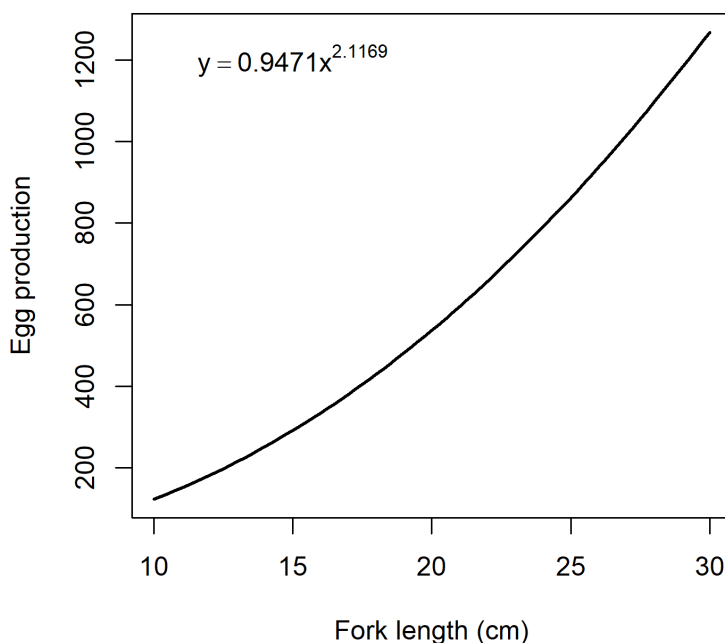


Figure 3. Relationship between female fork length and egg production from Scott Creek, CA (Shapovalov and Taft 1954).

The model assumes 1 redd per female spawner at an average size of 1.78 m² (SE = 0.14) (Gallagher and Gallagher 2005). Total spawning capacity is calculated within the model using a spawning habitat ratio requirement of 4:1 (Burner 1951); however, this calculation will assume uniform distribution of suitable spawning habitat within streams. We applied a hockey-stick function to limit spawners to spawning capacity and omit superposition or competition for spawning habitat.

Straying

According to Thorpe (1994), salmonids are famous for their homing precision and straying is usually regarded as a failure of individuals to achieve the population norm. However, without straying there would be no salmonid populations throughout much of their present range, as much of that area has been colonized by modern salmonids over the past 8000–15000 years (Thorpe 1994). Straying not only occurs in episodic pulses but also at relatively low and steady levels. Straying is important because it enables salmonids to colonize new areas over a relatively short time frame (Hendry et al. 2004; Quinn 2005), and is the behavior that has allowed salmonid populations over the course of thousands of years to colonize their existing habitats (Quinn 1984; Hendry et al., 2004), including establishing themselves within decades of glacial retreat (Milner and Bailey 1989; Milner and York 2001). Homing and straying are typically viewed as population-scale phenomena. According to Sandercock (1991), a return to the parental spawning ground provides a mechanism for enhancing survival by the repeat usage of good sites. Straying can also be a survival mechanism in that it may protect against the loss of an entire stock due to some environmental catastrophe in the home stream (Lieder 1989). It is clear that straying buffers against spatial and temporal variation in habitat quality and allows colonization of new habitats (Milner and Bailey 1989; Burger et al. 1997; Quinn et al. 2001; Stephenson 2006). Adults generally return to their natal streams to spawn, and stray rates are low in steelhead compared to other *Oncorhynchus* spp. (Westley et al. 2013). Straying rate estimates range from 1.2% to 11% in the Columbia River Basin and along the Oregon Coast (Keefer et al. 2005; Westley et al. 2013). The majority of straying occurs in non-natal tributaries within natal watersheds, however long-distance straying events (100 – 650km) can occur (Schroeder et al. 2001; Donohoe et al. 2021). Annual straying rates for the model were set to 5% (2.5% in either direction along the coast) with options to select values between 0% and 10%. For more detailed straying information, see the Natal Straying section withing Task 3.

Incubation

An estimated 97.5% of deposited eggs are successfully fertilized (Briggs 1953; Shapovalov and Taft 1954). Egg-to-fry survival estimates have ranged from 30% to 90% under controlled laboratory conditions (Shapovalov 1937; Shapovalov and Taft 1954) and 15% to 100% for steelhead in an in-river study of Central Valley steelhead (Merz et al. 2004); however, *in situ* estimates have been observed as low as 12% (Bley and Moring 1988). By default, egg-to-fry survival was set to 65%, based on populations in Humboldt County, CA (Briggs 1953), with options to reduce the survival to as low as 15% or as high as 90%.

Juvenile Rearing, Growth, and Outmigration

Juvenile steelhead typically rear in freshwater for 1 to 3 years after emergence (Shapovalov and Taft 1954). Estimated spring (February – April) growth for age-0 steelhead in Topanga Creek, CA is at least 24 mm and annually 61mm average (0.17 mm/day; Bell et al. 2011). These results are similar to estimates from the California Central Coast (Scott and Soquel creeks; Sogard et al. 2012) and but less than observed in the California Central Valley (Mokelumne and American rivers) (Sogard et al. 2012; Merz et al. 2016). Inhospitable conditions (e.g., low flows, high temperatures) in southern California can force early outmigration or encourage greater dependence on coastal lagoons or nearshore rearing (Moyle et al. 2008). Higher productivity in lagoons often leads to more rapid growth and increased survival (Smith 1990; Bond 2006; Hayes et al. 2008, 2011). A tagging study and analysis of scale morphology of returning adult steelhead in Scott Creek, CA showed that between 87% and 95.5% returning adults had reared in the lagoon, despite comprising less than half of the initial downstream outmigrants (Bond et al. 2008). For watersheds that form seasonal freshwater lagoons, an estimated 20% of fish are trapped when lagoons form and experience higher growth for an additional ~6 months, or until sandbars erode reconnecting the stream to the ocean (Smith 1990; Bond 2006; Hayes et al. 2008, 2011). Higher growth rates confer a survival advantage onto lagoon-reared fish by increasing their size at ocean entry (Bond 2006). Specific daily growth rates (% change in FL/day) for steelhead in Scott Creek, CA was 0.36 (SD = 0.20) in the lagoon compared to 0.06 (SD = 0.09) in riverine only individuals (Figure 4).

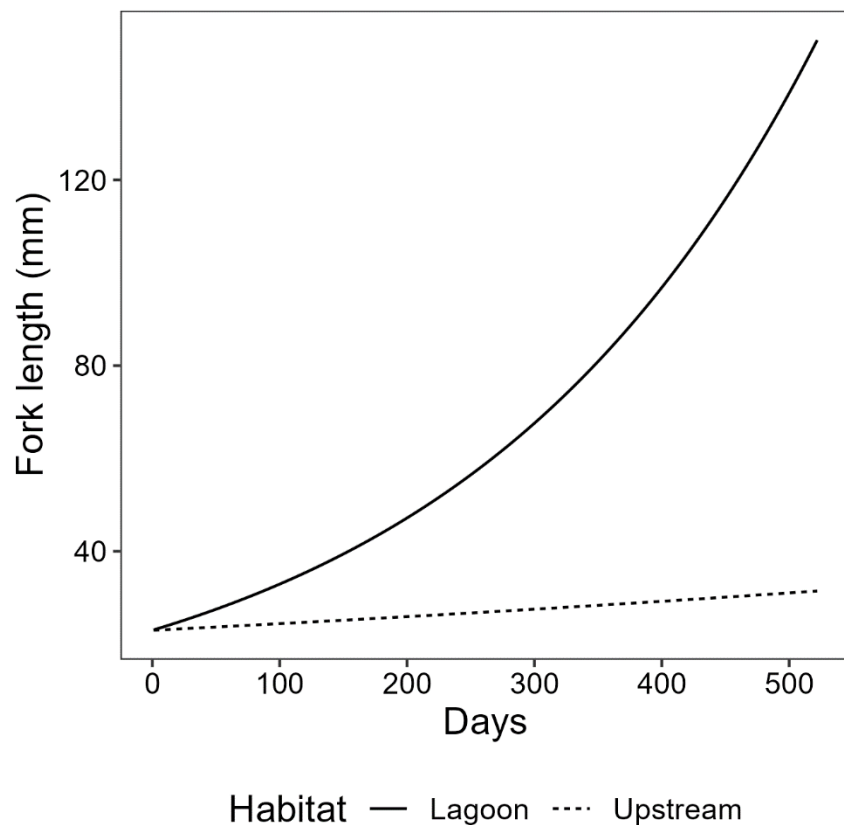


Figure 4. Simulated growth curves for juvenile steelhead rearing in lagoon and upstream habitats in Scott Creek, CA based on specific daily growth rates (Lagoon = 0.36 %FL/day, Upstream = 0.06%FL/day) presented in Bond (2006).

Data from an Above-Barrier Perched Resident population (see model framework for description) in middle Piru Creek also suggests populations dominated by younger age classes, with more than 90% of observations consisting of year-0 and year-1 juveniles and virtually no observations of age-5 or older individuals (Figure 5).

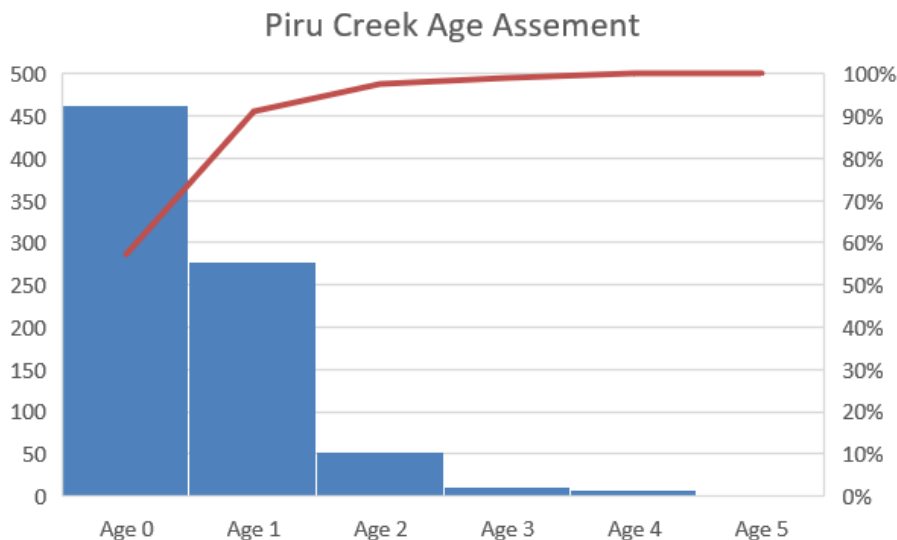


Figure 5. Age distribution of sampled fish at Piru Creek. United unpublished data from pre-implementation study.

Task 2: Identify and review available relevant models

Cramer Fish Sciences reviewed existing salmonid life cycle modeling frameworks to prepare for the development of the SCS Life Cycle Model. The purpose of reviewing existing modeling frameworks was to ensure the SCS LCM would be on par with the current existing life cycle modeling methods for Pacific salmonids. We drew heavily on examples from the Pacific Northwestern United States, where Chinook and steelhead life cycle models feature prominently in state and federal population management programs. The following sections summarize each of the different life cycle models we considered during development of the SCS Life Cycle Model.

Objective 2.1: Summarize/Evaluate general strengths and weaknesses

We identified four models previously built to evaluate salmonid population responses to management actions. Except for the Suisun Creek LCM, the models we reviewed were built specifically for Pacific Northwest rivers. Nonetheless, these LCMs provide a good general framework considering salmonid life cycle modeling.

Random Walk with Drift Model (Lindley, 2003)

The “random walk with drift” model (hereafter: the “Lindley model”), based on Lindley (2003) and parameterized with Central Valley field data for the 2007 and 2016 NMFS population viability criteria analyses (Boughton et al. 2007; Williams et al. 2016), is essentially a state-space model based on a simple exponential growth function (Equation 1).

Equation 1

$$N_t = N_{t-1}e^{r+\epsilon_t}$$

Where the number of individuals at time (N_t) is a function of the number of individuals in the previous time step (N_{t-1}) and the mean population growth rate (r). Random deviates (ϵ_t) in the mean population growth rate are added in each time step to create the “random walk” effect in population growth trajectories to represent process variance. The model can be modified (see Boughton et al. 2007) to simulate density-dependent growth.

State-space models are powerful modeling frameworks in ecology which link one or more mechanistic models (the process model) to an observation model (Patterson et al. 2008). The process model is usually some deterministic process which predicts the future state of some variable based on its current state. The predictions from the process model are then weighted by the likelihood of some observed data. Because the observation model essentially estimates the probability of observing some state, conditional on the ‘true’ state determined by the process model, state-space models offer a powerful way to handle uncertainty. Additionally, the process model can be parameterized with environmental data, providing an avenue for encoding realistic biological relationships into the model.

The Lindley model is broadly applicable; however, there are several drawbacks to the model and to the state-space modeling approach that should be considered. First, its process model (Equation 1) is fairly simple and assumes that population growth is not sensitive to age or stage-structure (Lindley 2003). Furthermore, the Lindley model does not consider alternative life history strategies (e.g., resident Rainbow Trout) or environmental influences. The Lindley model is capable of being expanded to include additional states and covariates; however, such an endeavor would require an advanced modeling approach and may include nested models. The parameters in state-space models (and in nested models generally) can be difficult to estimate, requiring maximum likelihood estimation (MLE) or a Bayesian Markov Chain Monte Carlo (MCMC) sampler (Patterson et al. 2008). Building the SCS LCM as a state-space model would provide a powerful tool for interrogating SCS population dynamics while explicitly incorporating uncertainty into the model; however, the current template (Lindley model) needs to be modified considerably to be able to incorporate all the desired life history stages, stage-transition processes, and environmental covariates. Thus, the model is liable to increase in complexity quickly and require advanced parameter estimation techniques (e.g., Kalman filtering, Bayesian MCMC).

Shiraz Model

The Shiraz model is based on a Beverton-Holt mortality function which adjusts life stage survival depending on life-stage specific relationships with environmental parameters. Movement between life stages can either follow an ideal free distribution to maximize fitness in the population, based on relative survival rates in different habitats, or occur in fixed fractions of the population. The Shiraz model also simulates hatchery operations and harvest policy and provides estimates of four important population criteria: abundance, productivity, spatial

structure, and life-history diversity. Furthermore, it provides a general modeling framework upon which many subsequent life cycle models have been at least partially based, including the NOAA HARP model and the CFS Nooksack LCM. The Shiraz model has several limitations, some of which have been addressed in subsequent modeling efforts, including a limited ability to model restoration actions, inability to predict increases in habitat quality as a consequence of increased habitat quantity, and reliance on fixed values for several model parameters. The Shiraz model therefore provides a foundation for model conceptualization, particularly in ensuring that the SCS LCM will be capable of properly assessing steelhead population viability.

NOAA Habitat Restoration Planning Model

The NOAA Habitat Restoration Planning (HARP) model is a multistage population dynamics model developed for Chinook, Coho, and steelhead in Pacific Northwest rivers that includes spatial, habitat, and life history components (Jorgensen et al. 2021). The NOAA HARP model receives spatial data as input, which are processed into habitat data layers to inform salmonid life-stage capacity and productivity relationships. Capacity is defined as the number of individuals a given habitat can support while productivity refers to population growth parameters such as fecundity and survival. Life-stage specific capacities and productivities depend on the habitat conditions present within the study system and may take on either fixed values or adjust dynamically according to either statistical or theoretical relationships to habitat-related variables (e.g., temperature, flow, fine sediments). The ensemble of data and functional relationships are then used to simulate cohort-based population growth on an annual time-step.

The model tracks annual cohorts as they move through individual subbasins and transition through various life-stages. The freshwater component of the model included nine life-stages: upstream migration, spawning, egg incubation, and age-0+ through age-2+ summer and winter rearing (Figure 6). Alternative pathways for smoltification occur within the model at age-1, age-2, or age-3 at which point smolts are subject to a delta-bay survival multiplier. Delta-bay survival is difficult to estimate *in situ*. Therefore, delta-bay productivity was back-calculated from smolt-to-adult return (SAR) rates reported in the literature by dividing the SAR by the age-weighted average ocean survival estimate.

Iteroparity in steelhead is handled in the NOAA HARP model by determining the cumulative respawn rate, determined by the product of the kelt rate, the ocean reconditioning rate, and the return rate.

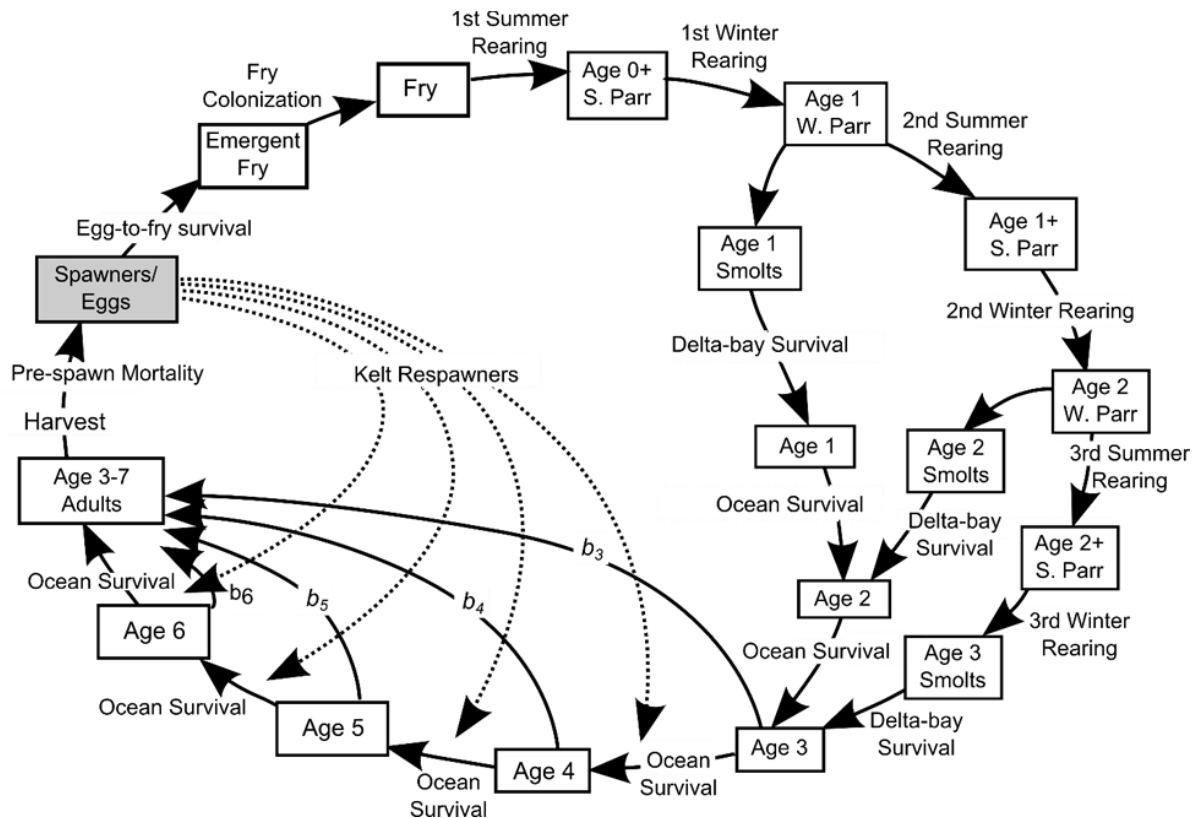


Figure 6. Steelhead life-cycle diagram developed for the Chehalis River basin (Jorgensen et al. 2021).

The NOAA HARP Model does not include a resident life history component and the capacities and productivities are tuned to reflect Pacific Northwest stream conditions. Nonetheless, it is one of the most comprehensive and transparent steelhead life cycle models and offers a solid frame upon which to base the SCS LCM.

CFS Nooksack Life Cycle Model

The CFS Nooksack LCM is largely based on the NOAA HARP model but includes several unique features. First, it utilizes a weighted connectivity matrix to account for spatial variation among populations and life stages, which allows for variable outmigration speeds in juveniles. Second, the CFS Nooksack LCM incorporates a highly detailed spatial layer of its watershed delineated at the reach scale for freshwater, estuary, and nearshore habitats. The CFS Nooksack LCM differs from the NOAA HARP model in the level of spatially explicit habitat detail built into the model, which allows for precise evaluation of life-stage specific population dynamics in response to habitat management scenarios and allows for complex population behaviors like straying. It is worth noting that this functionality was added to address specific issues observed within the Nooksack system that had previously been identified by regional experts and those familiar with the system.

CFS Suisun Creek Life Cycle Model

The CFS Suisun Creek Life Cycle Model is a cohort-based Steelhead LCM parameterized for a central California watershed. The focus was to determine the minimum spawning and rearing

habitat requirements needed to support a viable steelhead population in using a life cycle model approach. The model was parameterized with data from nearby central California watersheds whenever possible, and helped to highlight data gaps that would limit / improve the modeling effort over time. The LCM was automated as both a workbook model in MS Excel, as well as an R Shiny application to facilitate use, and help highlight model behaviors (E.g., loss of a population cohort). The model is simplified, and lacks spatial components for spawning, incubation etc. and relies on coarse assumptions, omitting flow, season, and habitat quality. That being said, the components are well described and identify areas of potential enhancement. This model serves as a good example of a focused LCM used to explore specific questions about known (potential) limiting factors, like available habitat, and provides many data sources that will be relevant for this work.

Objective 2.2: Pull together useful pieces into the best model framework

Models are most useful when they are developed to address specific questions (Rose et al. 2011). It follows that the technical details of modeling (e.g., scale and complexity) must be informed by the question(s) being asked. To that end, the SCS LCM is being developed to shed light on two key questions; the first question is asked at a population scale, the second at the watershed or subbasin scale:

1. How much does freshwater residency (e.g., Rainbow Trout) contribute to the overall population dynamics of SCS?
2. How does connectivity and/or drought affect population dynamics?

Here, it is important to distinguish between **prediction** and **forecast** modeling and between **relative** and **absolute** results (see Rose et al. 2011 for detailed discussion). **Prediction** models are used to determine some expectation under a specific set of conditions, which can be modified and compared across alternative scenarios. The results of such models are typically interpreted **relative** to a null model or some baseline modeling results. By contrast, **forecast** models are used to obtain the “best guess” results, and may be extrapolated beyond the range of observed data in an anticipatory manner. Such results can be considered **absolute** because they are supposed to represent an actual expected value. Because the two key questions posed are primarily concerned with understanding the relative contributions of freshwater residency and connectivity/drought to SCS population dynamics and not with estimating actual population abundances, prediction modeling is the most appropriate path forward.

We recommended that the SCS LCM be developed at the finest level of detail necessary to fully address the questions posed, but we caution against excessive complexity where it is unwarranted. The Lindley modeling framework is somewhat general, aimed at setting minimum viable population targets for the entire region, is not age- or stage-specific, and does not explicitly model life cycle processes. Furthermore, the Lindley model is more well suited for forecasting population abundances than it is for addressing the influence of life history and environmental factors on population dynamics. By contrast, the conceptual foundation established by the Shiraz model and adopted by the NOAA HARP and CFS Nooksack LCMs (from here forward, we refer to this suite of models as the “cohort-based life cycle simulation

models”) provides a flexible modeling approach well suited for addressing the key questions posed. The cohort-based simulation LCM approach merely requires a set of well defined, connected functional relationships and some initial conditions. Model results can be generated under alternative scenarios, potentially representing competing hypotheses, and compared relative to one another. An additional advantage of cohort-based simulation LCMs is that that they require less empirical data to produce useful results. Data-poor watersheds may produce imprecise or biased results; however, if the model and all its components are properly specified, its results can nonetheless provide valuable insights into the question being asked when interpreted properly (i.e., relative to a baseline). The Suisun Creek LCM serves as a good example of the application of a cohort-based simulation LCM.

We recommended adopting a modeling approach similar to that used in the Shiraz, NOAA HARP model, and CFS Nooksack LCM, all of which provide an appropriate scaffolding upon which to build the SCS LCM. The modular nature of cohort-based simulation LCMs means that model components can be easily tuned to specific study systems by incorporating data and parameter estimates from regional monitoring and/or studies. Further, the cohort-based simulation LCM framework allows for flexibility in spatial scale, which will enable us to build the model at the appropriate level of detail required to address the key questions without introducing unnecessary complexity. For example, the CFS Nooksack LCM incorporates a very fine level of habitat detail (reach-scale) beyond what is necessary given the purpose of this modeling study; however, the backbone of the model, and others like it, are its functional relationships representing the various life history stages and transitions which typically do not have any influence on scale. Because each process in a cohort-based simulation LCM runs in isolation, functional relationships can be easily added or removed representing productivity and survival at specific life histories and stages, and data can be leveraged from disparate sources to parameterize those relationships. Furthermore, existing code from the CFS Nooksack LCM, while currently built for Pacific Northwest Chinook, can be easily adapted, modified, and expanded in order to satisfy the goals and objectives of this study.

Task 3. Quantitative Life Cycle Model

Model Framework:

The goal of the Southern California steelhead life-cycle model (SCS LCM) is to understand the influence of source-sink dynamics between resident and anadromous *O. mykiss* on population viability (i.e., the 100-year extinction risk) for Southern California DPS populations, as well as the potential for long-term Southern California DPS persistence as a whole. The SCS LCM links individual life-cycle sub-models parameterized for three distinct life-history variants (Figure 7), The Anadromous population (A), Below-Barrier Freshwater Resident (R), and Above-Barrier Perched Resident (P) *O. mykiss* to a state-space model simulating exchange between populations and life-history variants (see definitions below). Exchange is dependent on habitat connectivity determined by instream flow and fish passage barrier ratings. The potential for spillover between populations within and between watersheds, and between life-history variants, is an important life-cycle dynamic not reflected in current SCS MVP size estimates for individual watersheds (i.e., 4,150 anadromous spawners per year on average; NMFS 2012). Our

model improves upon previous efforts to quantify the SCS MVP by considering the contributions of alternative life-history variants to the anadromous spawner population. By including a watershed scale spatial framework, MVP estimates can be obtained for individual watersheds to demonstrate their potential contributions to the population as a whole.

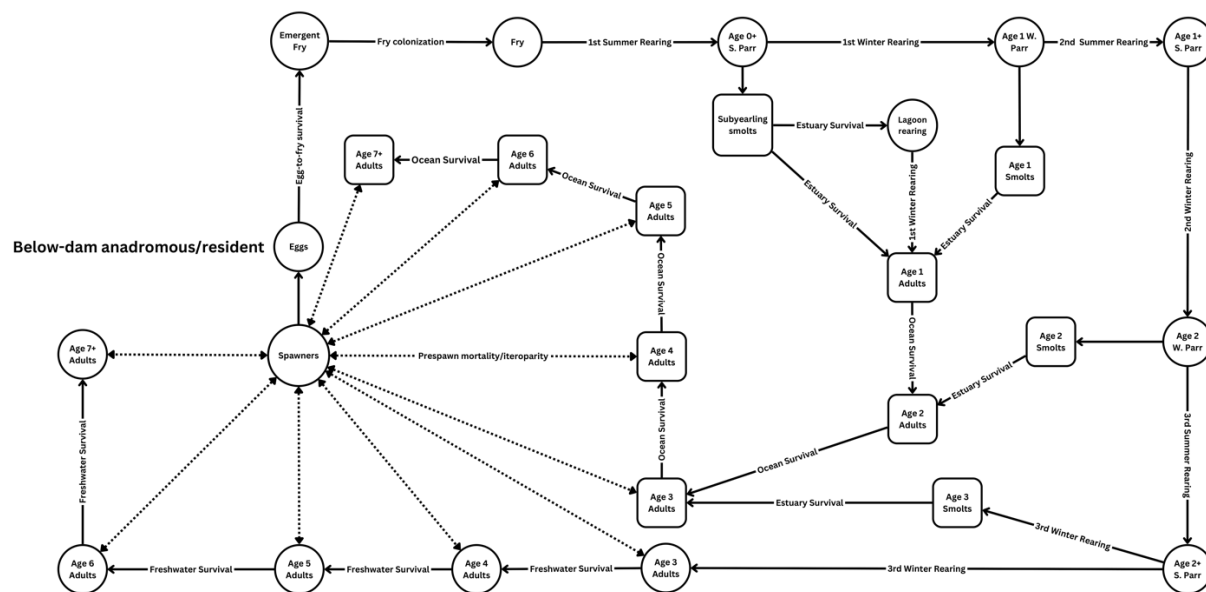


Figure 7. Conceptual life cycle diagram for Southern California steelhead which includes both freshwater (circles) and anadromous (squares) life stages.

Modeled Life Histories

As previously mentioned, this model considers three distinct life history variants that interact with each other to create the overall dynamics observed for the SCS population:

Anadromous (A) – Often referred to as the steelhead life history, these fish leave their natal basins and head out to the estuary and marine environment, where they rear for <1 to several years, before returning to spawn. They are affected by estuary and nearshore conditions, as well as the overall ocean conditions, and can exhibit straying behavior (see “Natal Straying” below).

Freshwater Resident (R) – The freshwater life history is often referred to as “Rainbow Trout” and represent fish that fully rear in freshwater. The Freshwater Resident population serves as the source of the Anadromous population, as all juveniles are considered freshwater residents until they smolt and head to the ocean.

Perched Freshwater Resident (P) – The perched freshwater life history represents freshwater residents that have no consistent connection to ocean, and therefore, cannot exhibit anadromous life histories outside of specific conditions (see Wet and Dry year effects below). Although this population does not directly affect the anadromous population, it can increase the freshwater resident population via spillover (R) which, in turn, effects the anadromous population (A).

By modeling all three life history variants simultaneously we are able to demonstrate complex population dynamics like reseeding and recolonization of extirpated habitats. When combined, we can demonstrate how *O. mykiss* adaptations, through life history variation, can extend the fitness and longevity of the overall population.

Modeled Basins

The SCS LCM considers multiple Basins within the DPS listing of SCS. The model is structured around the following river basins: Santa Maria River (Cuyama River and Sisquoc River as separate sub-basins), Santa Ynez River, Ventura River, Santa Clara River (with Piru Creek as a separate sub-basin), Los Angeles River, San Gabriel River, Santa Ana River, San Mateo Creek, San Luis Rey River, and San Diego River (Figure 8). Although each of the basins contribute to the population, the specific habitat and capacities vary widely, and necessitate separate parametrizations.

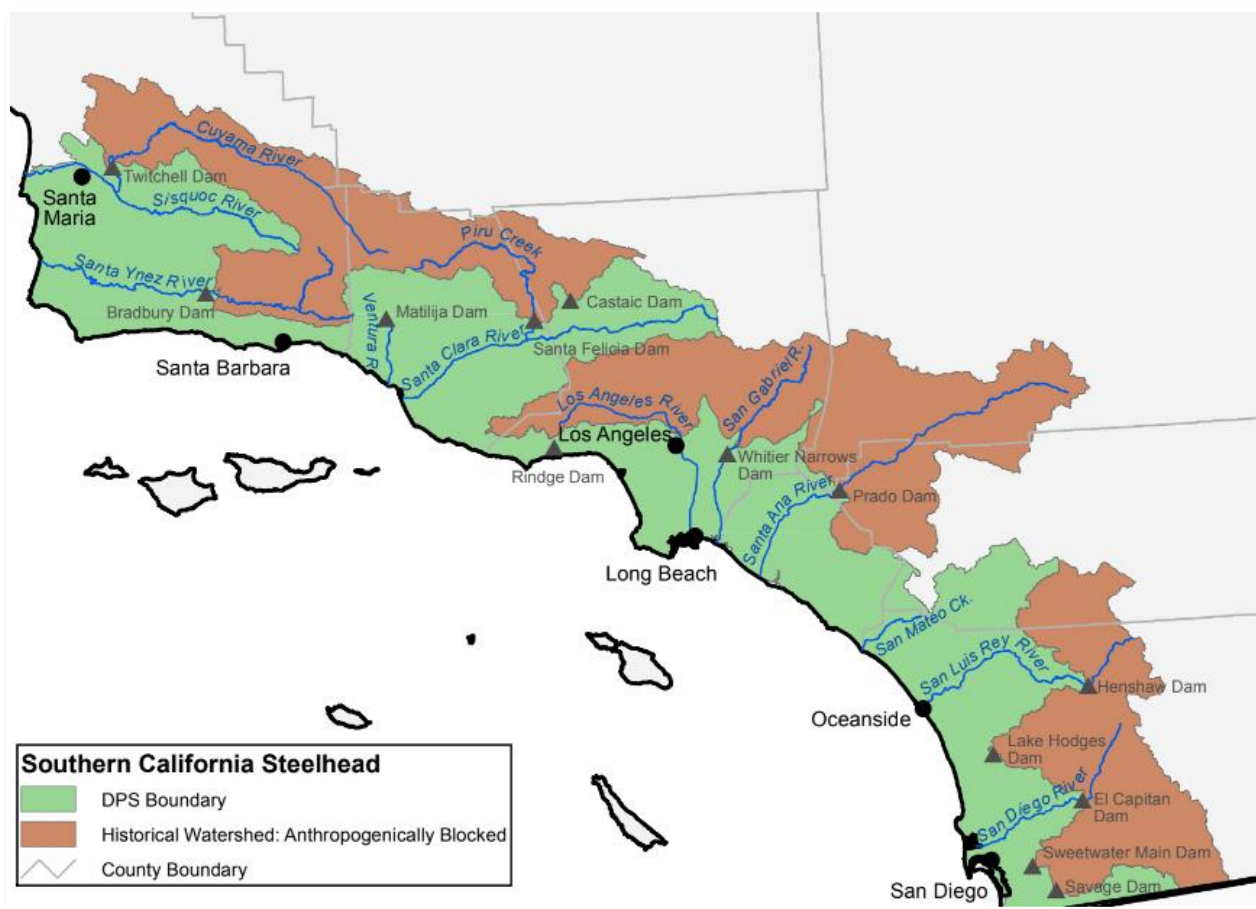


Figure 8. Basins modeled, and approximate extent of historical habitat. From NMFS 2016.

Natal Straying

Straying is typically defined as adult migration to—and attempted reproduction at—non-natal sites (Quinn 1993). Natal straying refers to the phenomenon where spawners do not return to their natal basin, but instead return to a nearby watershed to spawn. This process is responsible for recolonizing areas with previously extirpated populations and has been widely

documented amongst many species as an adaptation to density dependence or overall lack of quality habitat. For the SCS we model straying using a transition matrix that determines how much of a population might stray each year, and where they stray to. The transition matrix is an $n \times n$ matrix that represents all n watersheds. Each row represents a watershed, and values indicate what other watersheds (columns) receive straying. The diagonal of this matrix represents the amount of spawners that successfully return to their natal basin. Given limited data to parameterize the matrix, we have assumed small amounts of straying occur up and down the coast to adjacent watersheds, and that this rate may adjust based on available habitat (see dry year effects below).

Wet and Dry year effects

The model assumes three broad categories representing the overall hydrological conditions across the year: Wet, Regular, and Dry. These categories were determined by looking at historical records and binning model components and data into equal quantiles. Although this is aggregated and simplified classification, it allows us to incorporate and explore how wet and dry years can affect the population overall.

Regular Years- The model's default state assumes regular conditions. These conditions allow for anadromous connection and rely on the full reach capacities to drive density dependence. Perched populations have no emigration below blockages and remain "perched".

Wet Years- In wet years, we assume there is the opportunity for spill-over and downstream connection to anadromy for perched populations. In these years, we model volitional movement downstream of blockages by allocating the overage from the density dependent survival downstream into the resident population. This increase in resident population then also contributes to an increase in the anadromous population via the resident population smolt rate.

Dry years- In dry years, several adjustments are made. First, there is reduction in capacity for Freshwater and Perched populations representing both disconnection from habitat, as well as reduction of available habitat. Second, there are reduced smolting rates from resident populations to model the effect of disconnection to anadromous waters that can occur. Overall, these processes combine to have an overall negative effect on all three populations (perched, resident, and anadromous). Finally, following the assumptions of Quinn (1984) related to less stable streams in that we model an increase in straying rates in dry years to represent the potential disconnection from natal streams.

LCM Stages:

The state-space model moves fish through life stages (Figure 7) and records and reports metrics on an annual time step. Following is a brief description of how each transition occurs, and what values control it in the model.

- (A) Returns to Spawners:** Represents moving back to the natal spawning range and preparing to spawn. Reductions from both pre-spawn mortality, and harvest rate. Both factors are separated by LHP as well as region.
- (B) Spawner to Eggs:** Shifts successful return into spawners. Calculated using the Female ratio (fixed), as well as a hockey stick function for spawning capacity (separate for each LHP and region). Successful spawners are then converted to eggs via the fecundity parameter. Note, that successful spawners are not all removed from their population, see “Iteroparity” below.
- (C) Egg to Fry:** Egg survival and successful hatching into fry. Controlled by the ‘Egg to Fry’ parameter. Separate for freshwater and perched populations.
- (D) Fry Rearing and Colonization:** Fry survival to initial winter rearing. Controlled by the ‘Fry Survival’ parameter that represents the proportion of fry that survive. Separate for Resident and Perched populations. Reduced value in dry years.
- (E) Winter Rearing:** Density dependent reduction using Beverton-Holt based on capacity and productivity. Separate for Resident and Perched populations. Capacity and productivities by watershed and age. We assumed that the capacities by age account for effects of other age classes (NOAA HARP Model).
- (F) Summer Rearing:** Density dependent reduction using Beverton-Holt based on capacity and productivity. Separate for Resident and Perched populations. Capacity and productivities by watershed and age.
- (G) Smolting:** Rate that freshwater fish convert to Anadromous life strategies. Determined by smolt rates. Rates vary by age and potential to adjust for each watershed. Reduced values in dry years to represent disconnection to the anadromous floor. Only applied up to age 4.
- (H) Lagoon Rearing:** Specific adaptation strategy observed for anadromous population. Provides greater survival compared to estuary and nearshore rearing. Limited by lagoon capacity. Relies on density dependent curve to allocate population to lagoon (preferred), with overage rearing in estuary. Reduced lagoon capacities in dry years. We assume similar dynamics are at play for perched populations where reservoirs are present (Leidy 2004).
- (I) Estuary Survival:** Default conditions for anadromous rearing when lagoon area is unavailable/ occupied. Fixed rate that depends on age.
- (J) Ocean Survival:** Represents annual survival in the ocean using a fixed proportion. Separate values by age.

(K) Maturation: Rate that fish mature to spawners. Determined by maturation rates with separate rates for each LHP and age (fixed proportion).

(L) Adult Freshwater Annual Survival: Represents annual survival of freshwater adults. fixed rate. Separate value for resident and perched populations

(M) Iteroparity: Ability for spawners to return and spawn again next year. Controlled by iteroparity rate and respawn survival factor. Separate values for Resident and Perched populations. Assumes that a spawner's LHP is fixed and does not change on repeat spawning.

Initial conditions

The model requires initial conditions to seed the various populations. Long term dynamics are controlled by functional relationships and capacities, and are somewhat robust to initial conditions, however, the ramp up time to stable conditions will depend on the initial seeding and should not be overlooked. Given the potential for a 7-year anadromous return, we would not expect to hit stable dynamics in less than 10 years for most initial values. For this reason, the default model length is set to 125 years to account for the model's "warm up" time.

Demonstrated Population Dynamics – Useful tool without exact empirical data

As mentioned in the modeling section, one benefit of prediction models is the ability to compare a baseline scenario to alternate parameterizations to explore how changes in values (or assumptions) affect overall outcomes. Evaluating population dynamics often poses a challenge when empirical data is scarce or limited. In the case of the SCS population, the lack of empirical data has necessitated the use of a simplified model. However, despite these data limitations, we can still gain valuable insights by exploring how population dynamics are affected by individual modeling components and their values.

To that end, we have developed a model baseline scenario that serves as a fundamental starting point for our analysis. This model baseline parameterization not only helps us navigate the complexities of the SCS population dynamics but also serves as a crucial tool for demonstrating key phenomena in a controlled environment. While the model baseline scenario is an abstraction, it allows us to dissect and understand the impact of various factors, such as reproductive rates, mortality, and environmental variables, on population growth and sustainability.

These concepts, while derived from a simplified model, are robust and reveal core features of the model, and SCS adaptations. By focusing on these fundamental principles, we can uncover insights that may guide future data collection efforts or help refine more complex models as data becomes available. Thus, the use of the simplified model not only provides a pragmatic solution to data limitations but also offers a valuable framework for examining critical population dynamics and their sensitivity to different parameters and assumptions.

Impacts of Wet and Dry years

The model baseline assumes an ‘regular’ water year and has multiple parameters and capacities that are directly tied to ‘dry’ years to represent deleterious effects on the population. Similarly, ‘wet’ years offer opportunities for the perched population to ‘spill’ into connected freshwater habitat. The model’s default behavior assumes a sequence of water years that match historic trends, but the model also allows users to generate alternate randomized sequences to explore the impact of longer or shorter sequences of wet and dry years.

To emphasize these effects, consider the following parametrization. By setting the model to only include ‘Dry’ years, the perched population cannot contribute to the Resident population (and therefore the Anadromous population), and we can generate a downward trend for population, reaching an asymptote of the Perched population total (Figure 9).

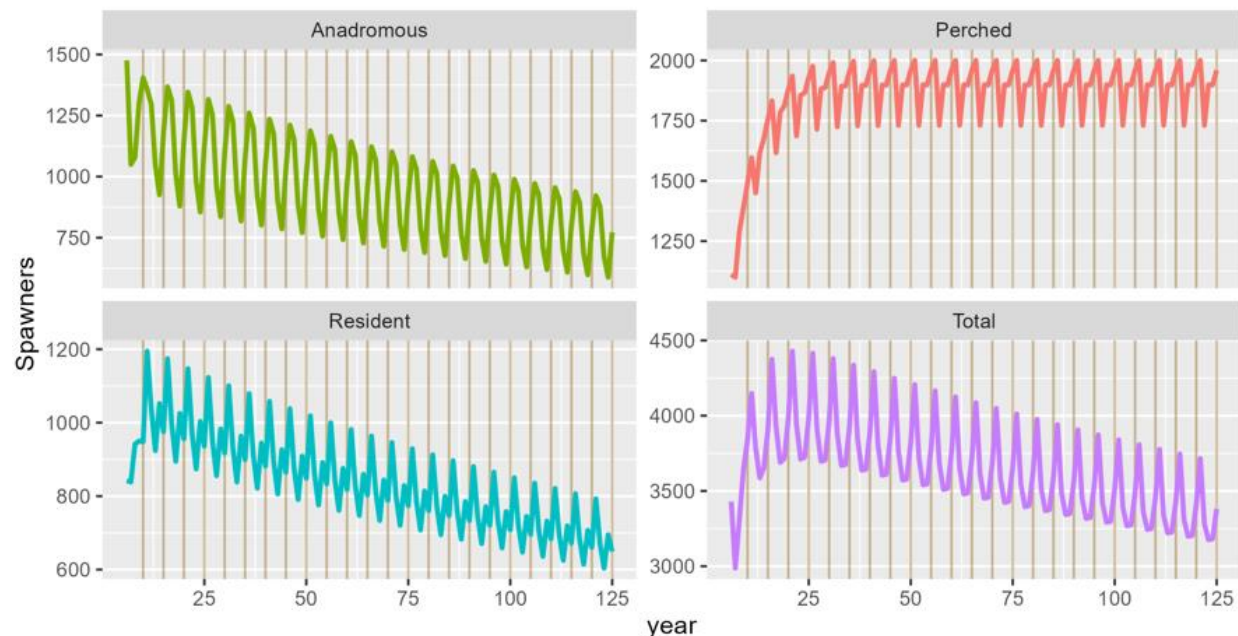


Figure 9. Example of Dry year effects. Plots of Spawners over time for the life history variants modeled in the SCS LCM, along with an aggregated total. Vertical brown lines represent ‘dry’ years in the run.

Introducing ‘wet’ years allows the perched population to contribute to the Resident population and can help offset the impacts of the ‘dry’ years in the run, eventually achieving values approaching MVP (Figure 10).

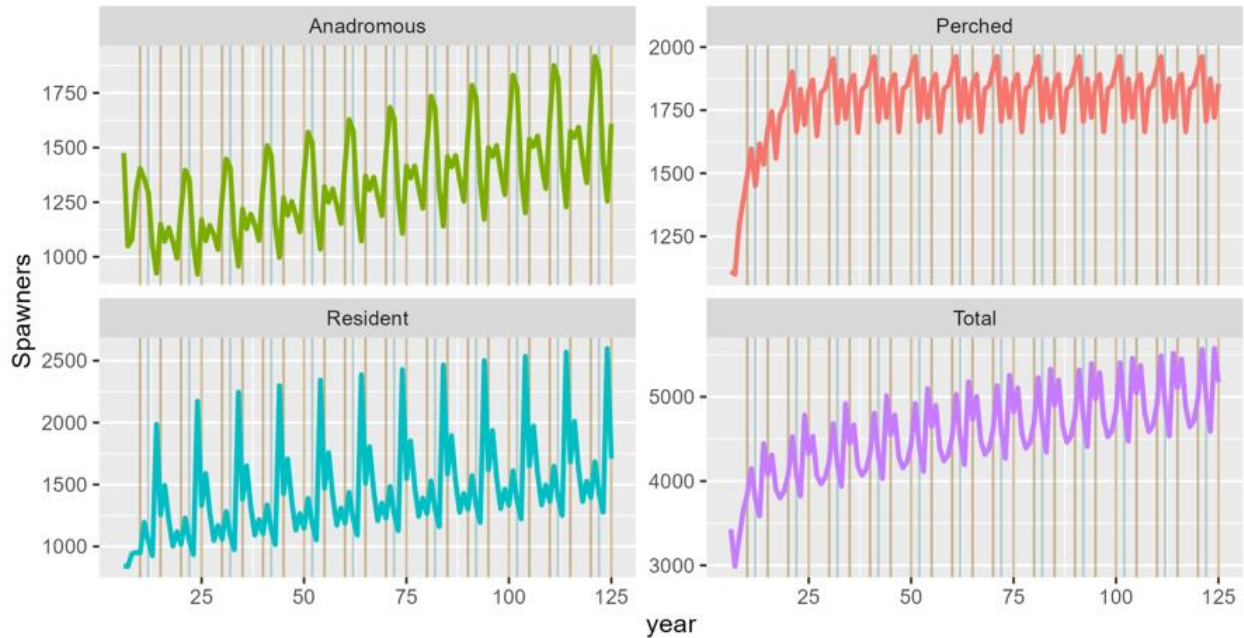


Figure 10. Example of Wet and Dry year effects. Plots of Spawners over time for the life history variants modeled in the SCS LCM, along with an aggregated total. Vertical brown lines represent 'dry' years in the run while blue lines indicate 'wet' years.

Reseeding Populations

Interchange between the resident and anadromous population allows for reseeding an extirpated anadromous population through smolting. Similarly, anadromous adults in the ocean may be able to reseed the freshwater resident population given their lagged return. Finally, the Perched population can reseed the resident population in wet years via ephemeral connections and spillover.

To highlight these dynamics, consider the following parametrization that extirpates the Resident and Anadromous populations after a series of 'dry' years, only to reseed the population from the perched population in a subsequent 'wet' year (Figure 11).

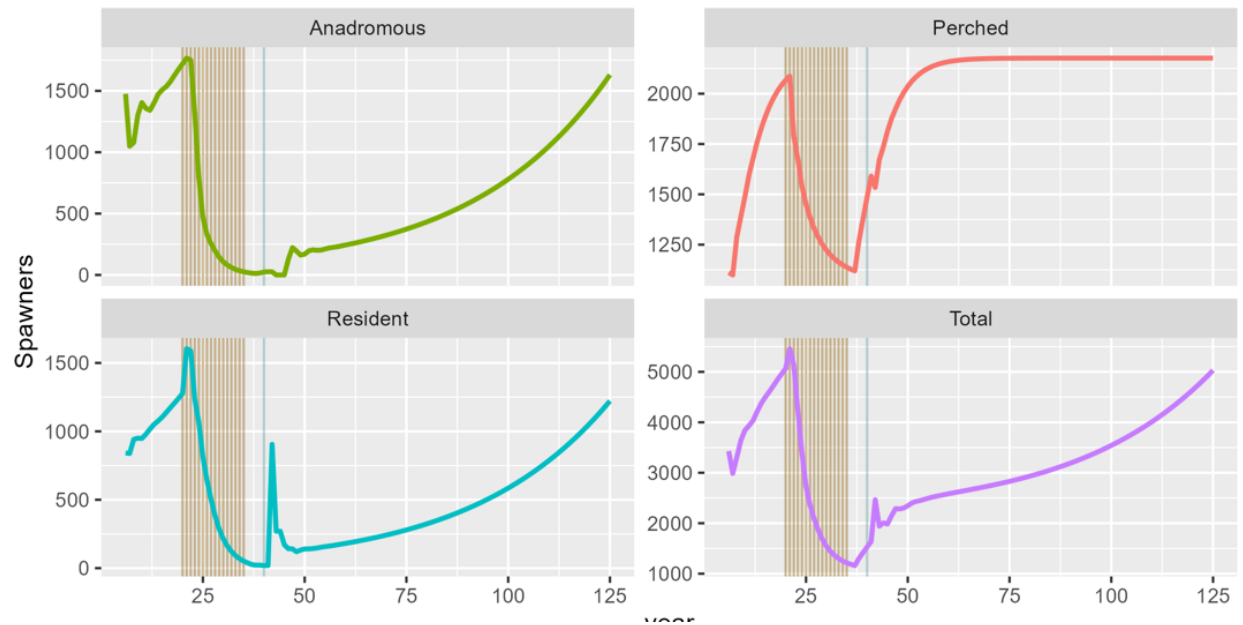


Figure 11. Example reseeding extirpated populations using interchange with a perched population. Plots of Spawners over time for the life history variants modeled in the SCS LCM, along with an aggregated total. Vertical brown lines represent 'dry' years in the run while vertical blue lines represent 'wet' years.

By including both 'wet' and 'dry' years, as well as the potential for interchange between populations, we can begin to produce complex population dynamics (Figure 12).

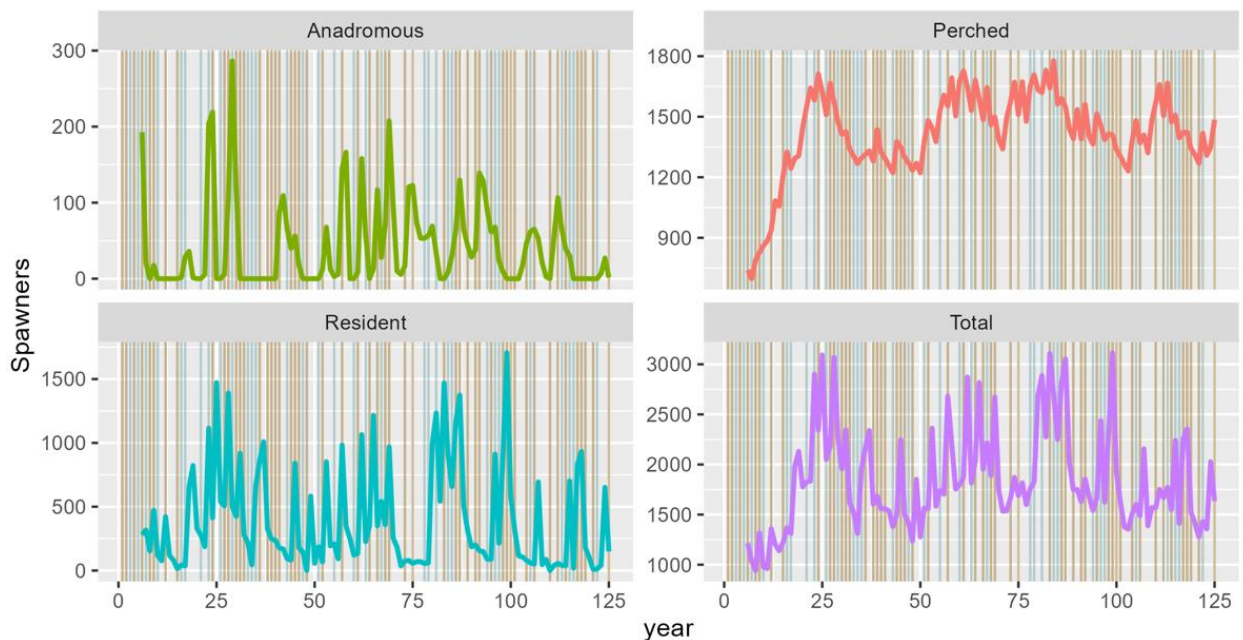


Figure 12. Example of complex populations dynamics by simulating a random sequence of water type years from an empirical distribution. Plots of Spawners over time for the life history variants modeled in the SCS LCM, along with an aggregated total. Vertical brown lines represent 'dry' years in the run while vertical blue lines indicate 'wet' years. Note the anadromous population being reseeded multiple times across the 125-year model run.

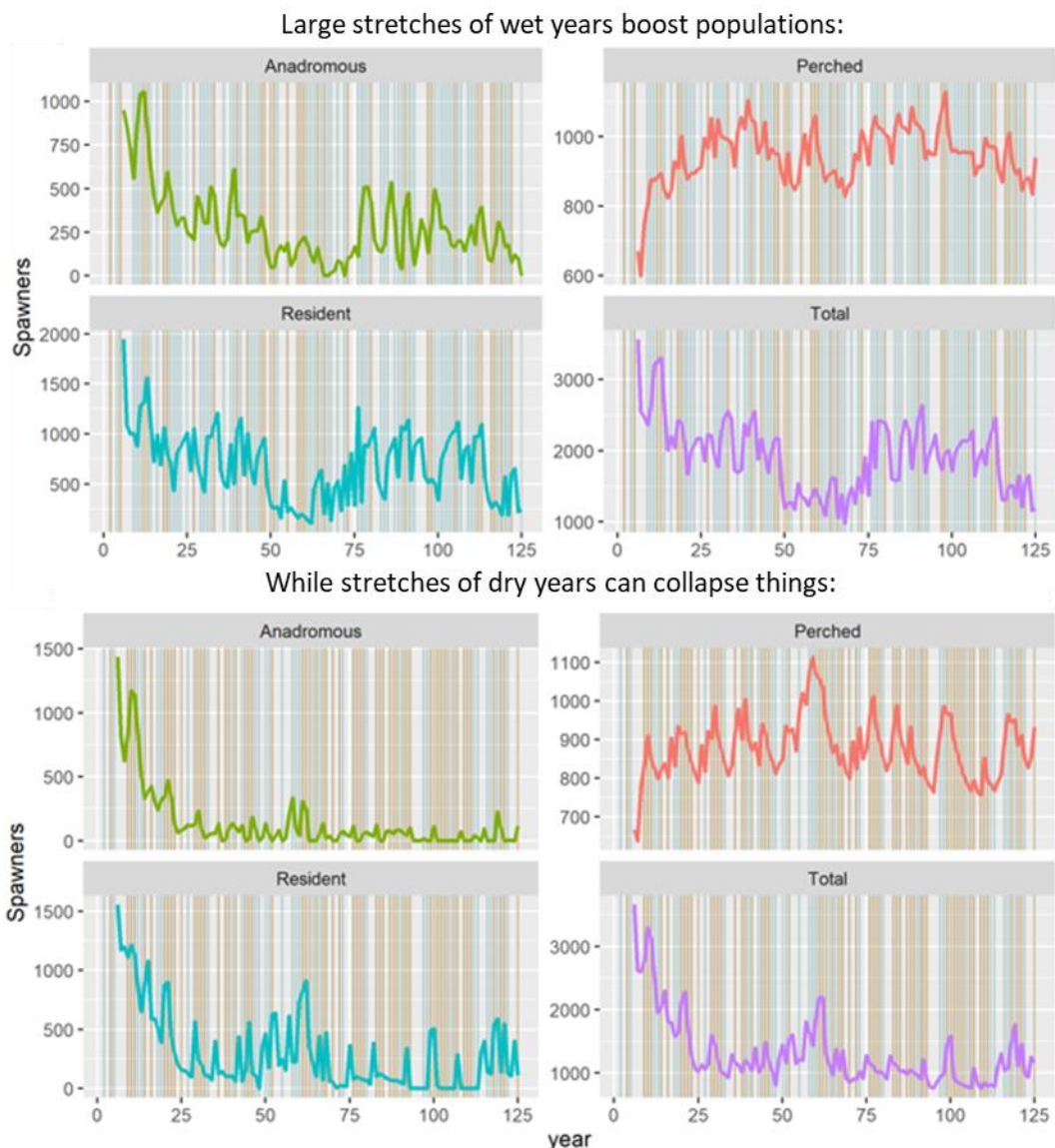


Figure 13. Further examples of complex dynamics demonstrating effects of wet and dry effects. Plots are the same as in Figure 12, but with larger stretches of Wet and dry years highlighting the importance of these environmental factors.

Recolonizing Extirpated Habitats

Beyond local interchange between Resident, Anadromous, and Perched populations, natal straying from the anadromous population can recolonize extirpated habitats. To demonstrate this, we created a diagnostic scenario that forces extirpation in a basin for a set of continuous years to highlight how recolonization can manifest (Figure 14). In the following example, Santa Clara River is recolonized from Natal Straying from nearby systems (Figure 14). Note that the model does not allow the upstream exchange of the Resident population to the Perched population (only the converse), and so the Perched population remains extirpated here:

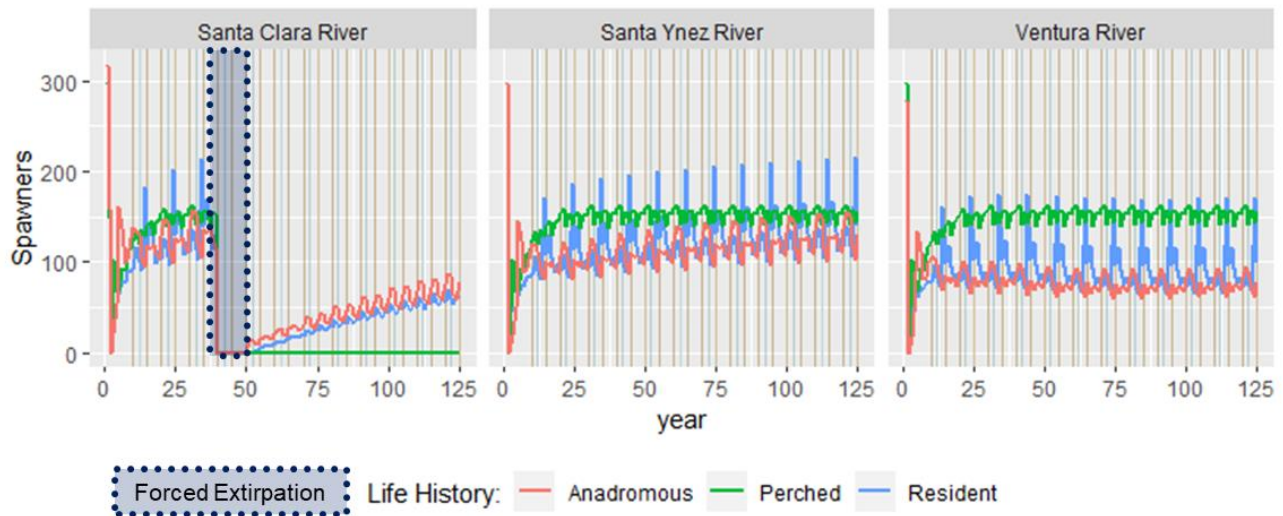


Figure 14. Example of recolonization of extirpated habitat by long-distance natal straying from alternate basins. Plots are of Spawners by year with three basins shown separately, with each Life History Variant distinguished by color. The shaded box represents a forced extirpation lasting 10 years. Vertical brown lines represent ‘dry’ years in the model while vertical blue lines represent ‘wet’ years. Note that the water year types match those presented in Figure 10.

Baseline scenario and default Parametrization:

For the model baseline scenario, we set the Anadromous return spawner total to just over the MVP needed to ensure genetic viability (~833 [2500 over 3 years for low extinction risk], Spence et al 2008), while aiming for a total population (including Freshwater and Perched populations) to exceed 4000 fish to achieve an MVP that is more robust to catastrophes and environmental stochasticity (Reed et al 2003 suggests ~5800). Finally, freshwater age structures will be calibrated to closely resemble empirical data from Piru Creek. This parametrization should highlight the overall contributions of the life history variants and connectivity to the long-term persistence of the DPS.

Model Implementation and Dashboard

The SCS LCM model has been implemented in R (R Core Team 2023, version 4.3.1) and only relies on well vetted packages that are available on CRAN with extensive histories of maintenance (“data.table”, and “ggplot2”). The model requires little computational resources to operate and should be able to run on most modern computers. Although the code is well commented, it can be intimidating to work with as it is a somewhat complex model relying on nested loops and complex accounting structures. To make the model as user friendly and transparent as possible, we have adapted the code into an R Shiny framework to create a reactive Graphic User Interface (GUI) to run the model (Figure 15). The GUI includes options to rapidly adjust the majority of the model’s parameters, and should allow novice users to explore the model, its assumptions, and results.

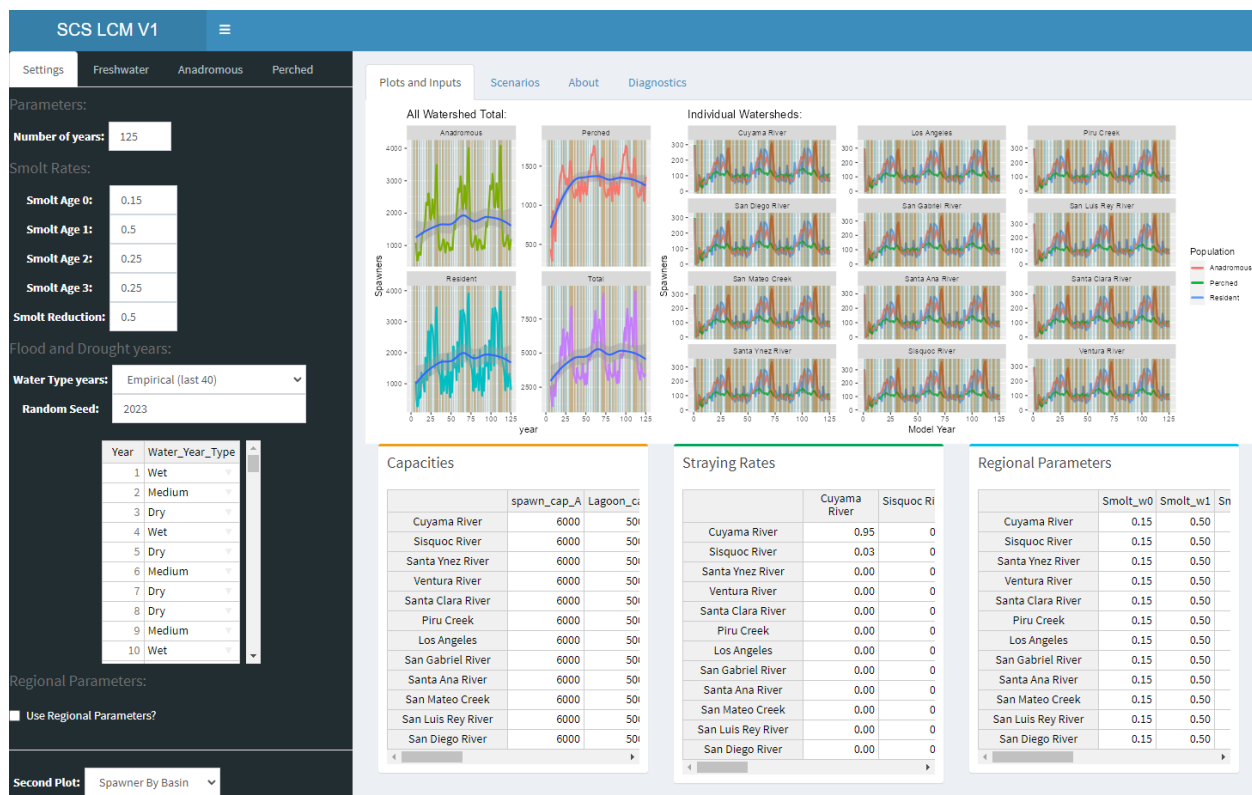


Figure 15. Screen capture of the GUI. A User guide for the model interface is under development and will be included in the 'About' tab.

Additional Scenarios

The model framework is easy to adapt and expand to consider other additional scenarios. As an example of this, we have added a “Reduction Event” scenario to the GUI (under the “Scenarios” tab in the main panel) that allows users to simulate a one-off large scale reduction event. Users have the option to select what year the reduction event starts, its total duration, and how large of a reduction in returning spawners should be applied. This sandbox scenario can help explore the effects of major unforeseen environmental impacts, and to evaluate population resiliency to these events. Moreover, this is meant to demonstrate the type of additional scenarios that can be created and evaluated using this model framework.

Concluding Remarks

- SCS show many adaptations and life history variants, many unique or emphasized for this population (e.g. Freshwater life histories, lagoon Rearing, ‘mini-jacks’, etc.). Ecological theory suggests that these adaptations are important to the population (hence their development) and should be considered in a population life cycle model to fully understand the dynamics of the population.
- Our model demonstrates how many of these adaptations can impact the long-term population dynamics, generally increasing the longevity and fitness of the population overall.

- Although the model is relatively simple and relies on many assumptions, the core dynamics demonstrate that concepts like connectivity (e.g., straying and perched population spill over) and life history variants (e.g., inclusion of both anadromous and resident spawners) can have relatively large impacts on a population's trajectories and persistence, and that omitting them may not fully capture the population's capabilities.
- By providing the GUI interface, the model can facilitate open discussion on management actions and future condition effects on the persistence of the SCS DPS at both regional and population wide scales.
- The model highlights data gaps and needs and can be updated as more information is available.

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