Limiting Factors Analysis for Trinity River Chinook salmon downstream of Lewiston Dam (*Oncorhynchus tshawytscha*) Using the Hamilton and Murphy Method

Technical Memorandum Prepared for:

Trinity River Restoration Program

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Table of Contents

1. Executive Summary

This report presents a limiting factors analysis (LFA) developed to determine why natural-origin Trinity River Chinook salmon *Oncorhynchus tshawytscha* are not meeting adult escapement goals and to identify which life stages and processes most strongly constrain population performance. The analysis uses a life cycle model to compare survival and production across the Trinity River, Klamath River, estuary, early marine period, and ocean, and to distinguish constraints that the Trinity River Restoration Program (TRRP) can manage directly from those requiring coordination or improved information. The results place TRRP actions within the full Chinook salmon life cycle and clarify how conditions within and beyond the Trinity River interact to influence adult returns.

Ocean harvest and survival after juveniles leave the Trinity River produced the largest modeled effects on naturally produced adult escapement. Reducing ocean harvest substantially increased modeled escapement and, in some scenarios, allowed the recovery target to be exceeded. Survival through the Klamath River, estuary, early marine period, and ocean also strongly influenced whether gains from Trinity River restoration translated into increased adult returns. Within the Trinity River, juvenile rearing habitat, survival, growth, and temperature were the strongest constraints directly managed by TRRP, although their effects on adult returns depended on downstream and marine survival. Spawning and incubation conditions affected production but did not explain most of the adult escapement gap under the scenarios tested; these factors may remain important in specific reaches, years, or disturbance conditions (e.g., fires, floods, etc.).

The nested limiting-factor scenario illustrates the relative magnitude and sequence of these constraints. Modeled mean pre-spawn adult escapement increased from 9,581 adults under baseline conditions to 37,520 after the tested ocean harvest and survival changes, to 53,908 after additional Klamath River disease and temperature improvements, and to 68,035 after additional Trinity River rearing survival, habitat, and temperature improvements. These cumulative results are diagnostic comparisons, not forecasts. Their apparent numerical precision reflects the specific model inputs and assumptions and should not be interpreted as precise predictions of future escapement. Instead, the pattern indicates that recovery likely depends on improvements across multiple life stages and spatial scales.

The strong effects of downstream and ocean conditions are biologically expected because Chinook salmon gain most of their adult biomass after leaving the Trinity River, and females acquire most of the energy reserves needed for egg production during that period. Under baseline

downstream and ocean conditions, modeled improvements in Trinity juvenile production alone produced relatively small increases in adult returns because survival later in the life cycle remained limiting. This does not lessen the biological importance of Trinity restoration. Trinity conditions determine how many juveniles enter downstream and marine habitats and influence their size, condition, migration timing, readiness for ocean entry, and life-history diversity. Producing more juveniles with a wider range of traits increases the likelihood that some will survive variable conditions, and these attributes will become increasingly important as climatic and hydrograph conditions become more variable.

TRRP's next phase should continue flow and habitat actions where the program has direct influence, use the life cycle model to compare alternatives before major restoration or operational investments, refine monitoring that informs management decisions and the LFA, and make coordination on downstream survival, ocean conditions, and harvest management a core component of recovery efforts. Success should be measured by improvements in juvenile size, timing, condition, life-history diversity, and later survival, rather than by habitat area or juvenile abundance alone. Priority information needs include habitat quantification and qualification for each Trinity life stage; survival in relation to juvenile size and migration timing; Trinity-origin survival through the Klamath River, estuary, and early marine period; current spawning and incubation conditions and egg-to-fry survival; fry-to-emigrant survival; adult holding behavior; and the production, timing, survival, and adult contribution of naturally produced yearlings. Addressing these gaps will strengthen the full-life-cycle basis of the LFA and increase the likelihood that freshwater restoration and management investments contribute to sustained adult escapement goals.

2. Key Terms and Acronyms

Acronyms and abbreviations used in the Technical Memorandum

Acronym / abbreviation	Definition
CDFW	California Department of Fish and Wildlife
cm	centimeter
Conf.	confidence in interpretation
GUI	graphical user interface
H_1–H_{20}	hypotheses 1–20
IDT	Interdisciplinary Team
LCD	life cycle diagram
LCM	life cycle model
LFA	limiting factors analysis
m^2	square meters
mm	millimeter
NOAA	National Oceanic and Atmospheric Administration
SAB	Science Advisory Board
SAR	smolt-to-adult return rate
TAG	Technical Advisory Group
TRRP	Trinity River Restoration Program

Term	Description / Standard Use
Alevin	A newly hatched salmon that remains in the gravel and relies on yolk reserves before emerging as a fry.
Adult escapement	Number of adult Chinook salmon returning to the Trinity River and available to spawn after harvest and migration losses. Use “adult escapement” for the abundance benchmark and “pre-spawn adult escapement” for adults present before spawning and before pre-spawn mortality is applied.
Adult immigration	Upstream movement of adult Chinook salmon from the Klamath River or ocean into the Trinity River. Use this term for the movement process; use escapement terms for adult abundance.
Baseline conditions	The calibrated model representation of recent or existing modeled conditions used as the reference point for diagnostic and scenario comparisons. Use “baseline conditions” rather than “current conditions” when referring specifically to model scenarios.
Calibration	Process of adjusting model parameters or assumptions so outputs reasonably match empirical observations. Use “calibration” for model fitting and “validation” only when independent data are used to evaluate performance.
Candidate limiting factor	A hypothesized factor, process, life stage, or transition that could constrain adult returns but has not yet been classified as primary, compounding, episodic, or non-limiting. Use this term before diagnostic evidence has been evaluated.
Cohort	A group of fish produced in the same brood year and followed through the life cycle.
Carryover effect	An effect of conditions experienced in one life stage that influences survival, growth, timing, condition, or reproductive success in a later life stage.
Compounding factor	A factor that reduces production, survival, or carryover traits but does not by itself explain the adult escapement gap under the scenarios tested.
Density dependence	A process in which survival, growth, or production changes as fish abundance approaches habitat capacity or resource limits.
Diagnostic test	A model run or analysis designed to isolate the influence of one life stage, process, or scenario on modeled adult escapement or key carryover traits.
Emergence	Movement of fry from gravel into the water column after incubation and yolk absorption.
Episodic factor	A factor that becomes important mainly during disturbance years, extreme environmental conditions, or narrow life-stage windows.
Equifinality	The condition in which different combinations of model parameters or assumptions produce similar model outputs, potentially leading to different interpretations of the processes limiting the population.
Escapement	Adult fish that escape harvest and natural mortality and return to the basin or spawning grounds. Use “adult escapement” for the adult escapement benchmark used in this report.
Fine sediment	Small sediment particles that fill spaces between spawning gravel, reduce intergravel flow and dissolved oxygen delivery, and can reduce egg incubation and fry emergence success when present at high levels.
Fry	A recently emerged juvenile salmon that has left the gravel and begun feeding and dispersing. Use “fry” for early post-emergence juveniles before parr markings and later rearing stages are emphasized.
Hatchery-origin	Fish produced in a hatchery and released into the river system. Use “hatchery-origin” when distinguishing hatchery-produced fish from natural-origin fish. Note that hatchery-origin adults that spawn naturally can produce natural-origin juveniles, while natural-origin adults used as broodstock can produce hatchery-origin juveniles.
Habitat capacity	The maximum number, biomass, or density of fish that available habitat can support during a specified life stage, location, and time period under defined flow, temperature,

	food, cover, substrate, competition, and survival conditions. Use "habitat capacity" as the general term; use life-stage-specific terms such as holding capacity, spawning capacity, or rearing capacity when the relevant life stage needs to be specified.
Holding capacity	The habitat capacity available to adult salmon during pre-spawn holding, especially spring-run Chinook salmon that hold for extended periods before spawning. Holding capacity depends on suitable depth, cover, thermal refuge, flow, spacing, disturbance, and survival conditions.
Hyporheic exchange	The movement of surface water into and through the streambed and back to the channel. In spawning areas, hyporheic exchange helps regulate dissolved oxygen, temperature, and waste removal around incubating eggs.
Expert-derived values	Interpretation or assumption development based on available empirical evidence, published literature, mechanistic understanding of Chinook salmon ecology, life-cycle modeling experience, and input from scientists familiar with the Trinity River system.
Graphical user interface (GUI)	The interactive interface used to run, view, and communicate model inputs, scenarios, and outputs without requiring users to work directly in model code. Spell out at first use; use GUI thereafter.
Juvenile rearing	The freshwater period when juvenile Chinook salmon feed, grow, seek refuge, and prepare for downstream migration. In this report, use "juvenile rearing" for the life stage affected by rearing habitat capacity, temperature, food availability, and density dependence.
Low-velocity habitat	Slow-water habitat such as channel margins, side channels, backwaters, and inundated floodplains used by juvenile salmon for feeding, refuge, and growth.
Juvenile outmigrants	Juvenile Chinook salmon leaving the Trinity River. Use this term for the fish themselves.
Juvenile outmigration	Downstream movement of juvenile Chinook salmon leaving the Trinity River. Use this term for the movement process.
Outmigration timing	The timing of juvenile Chinook salmon movement out of the Trinity River.
Migration corridor	The route fish travel through the Trinity River, Klamath River, estuary, and ocean.
Life cycle diagram (LCD)	The conceptual diagram showing Chinook salmon life stages, spatial areas, transitions, and life-history pathways used to structure the LCM. Spell out at first use; use LCD thereafter.
Life cycle model (LCM)	The deterministic, cohort-based model that links Chinook salmon abundance, survival, movement, and habitat capacity across life stages and spatial areas. Spell out at first use; use LCM thereafter.
Limiting factors analysis (LFA)	The diagnostic process used to identify which life stages, transitions, or factors most constrain adult Chinook salmon returns relative to objectives. Spell out at first use; use LFA thereafter.
Management priority	A factor or uncertainty that should guide action, monitoring, coordination, or scenario planning because of its expected biological effect, uncertainty, and TRRP role.
Natural production	Production of fish through natural spawning, incubation, rearing, and survival processes rather than hatchery release.
Outmigrant abundance	The number or estimated number of juvenile Chinook salmon leaving the Trinity River.
Natural-origin	Fish produced by natural spawning rather than hatchery release. Use "natural-origin" consistently when distinguishing naturally produced fish from hatchery-origin fish. Origin refers to where the fish was produced, not necessarily the origin of its parents: hatchery-origin adults can produce natural-origin juveniles if they spawn naturally, and natural-origin adults can produce hatchery-origin juveniles if they are used as broodstock in the hatchery.
Parameter	A model input, coefficient, or value that controls a biological, statistical, or functional relationship.
Parameterization	The process of assigning values, equations, or functional relationships to model parameters using data, literature, surrogate information, or expert-derived values.

Parr	A juvenile salmon that is actively rearing in freshwater and typically has vertical parr marks. Use “parr” for juveniles that are larger and more developed than fry but have not yet completed smoltification.
Pre-smolt	A juvenile salmon in transition between parr and smolt, often larger and later-outmigrating than fry or small parr but not yet fully physiologically prepared for seawater entry.
Pre-spawn mortality	Adult mortality that occurs after fish enter the river or holding areas but before successful spawning.
Primary limiting factor	A factor or life-stage constraint large enough, under the scenarios tested, to explain much of the adult escapement gap or to prevent achievement of the adult objective.
Reach-scale	Refers to conditions, estimates, or model inputs summarized for a defined river reach rather than a finer habitat unit or the entire basin.
Recovery target	The adult production or escapement objective used as the benchmark for evaluating whether modeled adult returns meet long-term program goals. Use “recovery target” consistently when referring to this benchmark.
Redd	A nest excavated by a female salmon in streambed gravel where eggs are deposited, fertilized, and incubated.
Redd superimposition	Construction of a redd over an existing redd, potentially displacing or damaging previously deposited eggs or embryos.
Rearing capacity	The habitat capacity available to juvenile salmon during freshwater rearing. Rearing capacity refers to the number, biomass, or density of juveniles that available rearing habitat can support under specified flow, temperature, food, cover, competition, and density-dependent survival or growth conditions.
Scenario	A defined combination of model inputs or assumptions used to evaluate a hypothesis, management action, uncertainty, or environmental condition.
Sensitivity analysis	Evaluation of how model outputs change when parameters, assumptions, or structural choices are varied.
Smolt	A juvenile salmon that has developed the physiological, behavioral, and morphological traits needed for downstream migration and transition to estuarine or marine environments.
Smoltification	The physiological and behavioral transformation that prepares juvenile salmon for seawater entry, including changes in osmoregulation, body form, coloration, movement tendency, and downstream migration readiness.
Pre-spawn adult escapement	Adults that have returned to the Trinity River before spawning and before accounting for pre-spawn mortality. Use “pre-spawn adult escapement” when referring to adults entering or present in the Trinity River prior to spawning.
Spawning capacity	The habitat capacity available for successful spawning, including the number of redds, females, or effective egg deposition that can be supported without excessive density effects, redd superimposition, poor substrate conditions, or reduced fertilization and incubation success.
Spawning gravel	Gravel used by spawning salmon to construct redds and incubate eggs. Suitability depends on particle size, permeability, stability, depth, flow, and the ability of females to excavate redds.
Spawning escapement	The subset of adult escapement that survives to spawn. Use “spawning escapement” when distinguishing adults that successfully spawn from pre-spawn adult escapement.
Subyearling	A juvenile salmon that migrates or is sampled during its first year of life. Use “subyearling” for age-0 fish, including fry, parr, pre-smolts, or smolts depending on development stage.
Stock-recruitment relationship	The relationship between the abundance of spawning adults and the number of resulting offspring or recruits produced at a later life stage.
Surrogate data	Data from another river, population, species, study, or modeling framework used when Trinity-specific information is unavailable or insufficient.
Smolt-to-adult return rate (SAR)	The proportion of juvenile salmon leaving freshwater or entering the ocean that survive to return as adults. Spell out at first use; use SAR thereafter.

Thermal regime	The spatial and temporal pattern of water temperature that affects salmon growth, survival, disease risk, migration timing, and habitat suitability.
Thiamine deficiency	A maternal nutritional deficiency that can reduce egg viability, embryo development, or early fry survival. In this report, treat thiamine deficiency as an episodic or condition-dependent incubation stressor unless stronger Trinity-specific evidence indicates otherwise.
Yearling	A juvenile salmon that remains in freshwater for at least one full year before migrating. Use “yearling” for age-1 fish and distinguish it from subyearling migrants when discussing life-history diversity and data gaps.
Uncertainty	Incomplete knowledge about data, parameter values, model structure, biological mechanisms, or future environmental conditions that affects confidence in interpretation.
Transition	The change from one life stage to the next, commonly expressed as the proportion of fish that survive or are produced from one stage to the next. Comparing transition rates helps identify where survival or production may be limiting across the life cycle (Merz et al. 2013).
Trinity River Restoration Program (TRRP)	The multi-agency program responsible for implementing Trinity River restoration and adaptive management.

3. Report Organization and Supporting Materials

The main text presents the management context, analytical approach, principal results, priorities, and recommendations. Technical details are consolidated by purpose: Appendix A documents model structure and transitions; Appendix B documents the Phase 2 model implementation, including model logic and assumptions, data used, LFA test procedures, and expected test results; Appendix C preserves the Phase 1 scoping information, including potentially useful data for each transition, candidate drivers and limiting factors, preliminary data requests, and proposed uses of datasets; Appendix D presents calibration and sensitivity analyses; Appendix E provides expanded results and figures; Appendix F summarizes data gaps and uncertainties; Appendix G provides the user guide; and Appendix H provides a table of model parameters, input values, and corresponding references. Each main-text section directs readers to the specific appendix containing its supporting evidence.

4. Introduction

The Trinity River Restoration Program’s (TRRP) strategy originated in the 1988 restoration framework and the Trinity River Flow Evaluation Study, which identified altered flow and sediment regimes, channel simplification, and limited juvenile rearing habitat as major effects of Trinity River Division operations. These findings established managed flows, sediment management, channel rehabilitation, and expansion of juvenile rearing habitat as the program’s principal restoration tools. However, continued shortfalls in natural-origin adult escapement indicate that population performance must be evaluated across the full Chinook salmon *Oncorhynchus tshawytscha* life cycle, including stages downstream of the restoration reach and in the ocean. This limiting factors analysis (LFA) was therefore developed to test where low survival or production is sufficient to explain the adult escapement gap, determine how constraints shift when conditions improve, and distinguish factors TRRP can manage directly from those requiring coordination, monitoring, or revised expectations.

Through its Science Plan and adaptive management program, TRRP identified the need for an LFA to address a persistent uncertainty: why adult returns remained low despite more than 20 years of restoration investment and documented increases in juvenile production. The LFA was conceived as a structured, life cycle-based evaluation to identify and rank constraints on population performance, quantify their relative influence, and provide a scientific basis for prioritizing future management and restoration actions.

This technical memorandum presents the LFA for natural-origin Trinity River Chinook salmon produced downstream of Lewiston Dam. The analysis follows salmon through the full life cycle to identify where low survival or production most limits adult escapement and whether plausible improvements could meaningfully increase returns. It also distinguishes factors that the TRRP can manage directly, influence through coordination, or account for in planning, and documents major evidence gaps and uncertainties. Consistent with the Phase 2 work plan, the project uses an open-source life cycle model (LCM) and graphical user interface to test explicit hypotheses, compare management and environmental scenarios, document model structure, assumptions, data, uncertainty, calibration, and diagnostic results, and identify priorities for restoration, monitoring, and future model testing. The resulting model, graphical user interface, and supporting documentation provide transparent tools that TRRP can update as new information becomes available.

5. Study Context and Management Relevance

TRRP is a long-term, multi-agency effort established to restore the Trinity River's form and function and recover anadromous fish populations downstream of Lewiston Dam, particularly Chinook salmon, coho salmon *O. kisutch*, and steelhead *O. mykiss*. The program was developed to mitigate effects of the Trinity River Division of the Central Valley Project, including reduced annual flows, disrupted sediment transport, simplified channel and floodplain processes, and degraded salmonid habitat.

The 1988 restoration framework identified reduced sediment supply, channel simplification, and limited juvenile rearing habitat as major consequences of Trinity River Division operations. That diagnosis established the historical emphasis on gravel and sediment management, channel rehabilitation, managed flows, and expansion of juvenile rearing habitat that continues to guide TRRP actions (U.S. Fish and Wildlife Service 1988).

The current management context also reflects a longer history of watershed and fishery alteration preceding and following dam construction. In the Trinity Basin, extensive gold mining beginning in the mid-1800s, followed by logging and associated sediment inputs, degraded channel and floodplain conditions well before completion of the Trinity River Division (TRRP 2026; U.S. Fish and Wildlife Service 2026). Construction of Trinity and Lewiston dams in the early 1960s then blocked upstream habitat and substantially reduced instream flows through large interbasin water exports, while hatchery production was expanded as a mitigation measure for lost habitat and fish production (U.S. Department of the Interior 2000; U.S. Bureau of Reclamation 2017; CDFW 2026). Harvest and other downstream pressures have also continued to influence adult returns. Together, these historical and ongoing stressors help explain why the LFA must evaluate multiple life stages and distinguish between constraints that remain directly manageable within the Trinity River and those shaped by broader basin or ocean conditions.

Climate-sensitive conditions, including water temperature, snowmelt timing, low-flow periods, wildfire and sediment pulses, disease risk, estuary conditions, and ocean productivity, are treated as background drivers that can amplify or dampen life-stage responses. They are not evaluated as a separate limiting factor, but they inform scenario testing and help set realistic expectations for how Trinity River actions translate into adult returns.

The TRRP's long-term goals are to restore the attributes of a healthy, functioning alluvial river system in the approximately 40-mile reach between Lewiston Dam and the North Fork Trinity River while increasing natural production of anadromous fish and supporting tribal, commercial, and recreational fisheries. Consistent with the Trinity River Record of Decision and related synthesis work, long-term recovery objectives aim to rebuild Chinook salmon populations to levels sufficient to support substantial natural spawning escapement while also providing harvest opportunities for tribal, commercial, and recreational fisheries, reflecting a dual goal of ecological recovery and sustainable fishery yield. Long-term average annual adult production goals generally include 62,000 fall-run Chinook salmon, 6,000 spring-run Chinook salmon, 7,500 coho salmon, and 22,000 steelhead, reflecting the adult production needed to offset habitat blocked by Lewiston Dam and related Trinity River Division impacts (U.S. Department of the Interior 2000; CDFW 2026; U.S. Fish and Wildlife Service 2026).

Within that adaptive management context, the Chinook salmon LFA is intended to evaluate where constraints remain across the full life cycle so the program can better understand why restoration actions in the mainstem have not yet produced the full population response needed to meet long-term fishery goals. This is especially relevant because TRRP's mandate is not only to improve river form and habitat conditions, but also to restore and sustain natural production of anadromous fish populations through an integrated strategy of flow management, channel rehabilitation, sediment management, watershed restoration, hatchery management, and monitoring-based adaptive management (Pickard et al. 2022).

The analysis diagnoses which life stages and processes most strongly constrain population performance rather than simply cataloging all possible stressors or treating unmet escapement targets only as an endpoint. Following Hamilton and Murphy (2018), the LFA treats the adult shortfall as a symptom and asks which life stage or transition is failing strongly enough to create that gap. In practice, the analysis narrows attention to the few stages most plausibly limiting adult returns (relative to recovery targets), using available data where possible and structured expert-derived values where information is weak, indirect, or absent. The memo also distinguishes, where feasible, between constraints that Trinity River managers can directly influence through flow and habitat actions and constraints that occur downstream, in the Klamath River, or in the ocean and therefore lie partly or wholly outside Trinity River management control. This distinction is essential for both prioritization and expectation setting.

Within that broader context, several stressors remain especially relevant to Trinity River Chinook salmon recovery. The most direct effects of Trinity River Division operations include restricted access to historical upstream habitats, increased spatial overlap between spring- and fall-run populations, altered hydrology, reduced peak and seasonal flow variability, loss of coarse spawning gravel and increased fine sediment storage, simplified channel and floodplain structure, impaired temperature dynamics, and reduced access to low-velocity rearing habitat and other floodplain features needed by juveniles (U.S. Department of the Interior 2000; U.S. Bureau of Reclamation 2017; TRRP 2026). These changes can reduce spawning success, constrain juvenile growth and rearing capacity, increase overlap in spawning and rearing areas, and alter the timing, condition, and survival of emigrating fish. Hatchery production is also part of the recovery context because hatchery-origin and natural-origin Chinook salmon mix in natural escapement, complicating interpretation of natural production and highlighting the need to track potential ecological and genetic interactions (TRRP 2026; Gough et al. 2026; Kier et al. 2023). More recent restoration and monitoring results indicate that managed flow releases, gravel augmentation, and channel rehabilitation are intended specifically to reverse these effects by improving channel processes, spawning substrate, temperature and habitat conditions, and juvenile rearing opportunity (TRRP 2026; U.S. Fish and Wildlife Service 2026). Available program summaries also indicate that juvenile abundance gains do not necessarily imply full demographic recovery if fish remain small, habitat access remains limited, or mortality shifts to downstream and later life stages.

The LFA examines the life stages and processes included in the current Chinook salmon model. It considers harvest, hatchery operations, river flow, water temperature, habitat, conditions in the lower Klamath River and ocean, and major disturbances when they help explain where salmon survival is lowest or where management could make a difference. Some factors could not be tested separately because there was not enough Trinity River-specific information or the model did not represent them as separate processes. Their effects may instead be included in the model's overall survival estimates for broader life stages.

6. Analytical Framework

6.1 Conceptual approach

The Trinity River LFA applies the life-stage-based framework of Hamilton and Murphy (2018) to diagnose two central management questions: why Trinity River Chinook salmon persistently fail to meet escapement goals and which life stages most strongly suppress adult returns. The model represents pre–Klamath River dam-removal conditions; assumptions about downstream habitat, temperature, disease, and survival should be revisited as post-removal data become available.

Potential stressors are evaluated as candidate causes of poor performance at specific life stages, but a stage qualifies as limiting only when observed or inferred survival is sufficiently below the rate needed to meet escapement objectives and a plausible improvement materially increases adult returns. The analysis distinguishes flow-related, non-flow-related, and interactive factors and identifies whether each constraint falls within TRRP management authority, can be influenced through coordination, or can only be monitored and incorporated into planning.

Conditions at each life stage can affect salmon survival later in life. Chinook salmon gain most of their adult body mass in the ocean, and females build most of the energy reserves needed to produce eggs after leaving freshwater (Wells et al. 2008). The model's large effects of ocean survival and harvest are therefore biologically expected. However, freshwater conditions determine how many juveniles reach the ocean and influence their size, health, migration timing, readiness for ocean entry, and range of life histories. These characteristics can affect survival in downstream waters and the ocean (Sturrock et al. 2015; Chasco et al. 2021). The analysis therefore considers both survival during each life stage and how freshwater conditions may affect salmon later in life, rather than treating freshwater and marine conditions as unrelated.

A LFA identifies the life stages that most restrict population recovery rather than attempting to simulate every process affecting salmon (Hamilton and Murphy 2018; Booth et al. 2016). The LCM supports this diagnosis by following changes in survival, movement, and abundance from one life stage to the next (transition) (Merz et al. 2013; Hamilton and Murphy 2018; Jorgensen et al. 2021; Kendall et al. 2023). The analysis first compares current or estimated performance at each stage with the performance needed to meet adult escapement goals. It then tests where mortality or low production may be concentrated and whether a plausible improvement at that stage would increase adult returns. The analysis focuses first on stages with the strongest evidence of limitation and can incorporate new hypotheses, data, and revised assumptions as they become available. Section 6.2 describes the step-by-step method used in this report.

6.2 Hamilton and Murphy method

Hamilton and Murphy (2018) provide a step-by-step method for identifying why a population is not meeting its goals. For Trinity River Chinook salmon, the analysis begins with the adult escapement goal and measures the shortfall. It then follows salmon through each life stage (life stage transition) and asks where survival or production is too low to meet that goal. A life stage is considered limiting only if improving conditions at that stage would meaningfully increase adult escapement. Trinity-specific data are used when available. When local information is limited, the analysis uses data from comparable river systems, published studies, established biological relationships, and checks that results are consistent across the salmon life cycle. Where important information is still missing, expert-derived values document assumptions and identify the data most needed to improve the analysis (Roni et al. 2018; Jorgensen et al. 2021). The Trinity LFA generally follows Hamilton and Murphy's life-stage, cause-and-effect, and repeated-testing method. However, because Chinook salmon use river, estuary, nearshore, and ocean habitats, and Trinity River-specific data are not available for every life stage, the analysis compares model scenarios and combines available evidence rather than using formal statistical tests for every question.

A key feature of the Hamilton and Murphy approach is that potential limitations are tested repeatedly rather than ranked only once. The analysis first identifies the life stage or transition most likely to explain the adult escapement gap. It then improves that stage or transition in the model and asks whether the population reaches its goal or whether another part of the life cycle becomes the next important constraint. Repeating this process helps distinguish primary limiting factors from factors that add to the problem, become important only under particular conditions, or have smaller effects. For the Trinity River, the same process also separates constraints that managers can address directly within the Trinity River from those that occur later in the Klamath River, estuary, or ocean.

In practice, the method defines the adult escapement gap, maps the life cycle, tests candidate constraints by life stage, and then relaxes the strongest apparent constraint to see what becomes limiting next. Factors are then interpreted by biological effect, uncertainty, and whether TRRP can manage, influence, or only monitor them. Priorities should therefore change as new data, scenarios, or review comments improve the diagnosis.

For the Trinity application, a Technical Advisory Group (TAG), primarily composed of TRRP Interdisciplinary Team (IDT) and Scientific Advisory Board (SAB) members, helped compile and evaluate available Trinity River-specific and surrogate-system information (Figure 1). Section 8 and Appendix C describe the data-source hierarchy and supporting workflow in detail.

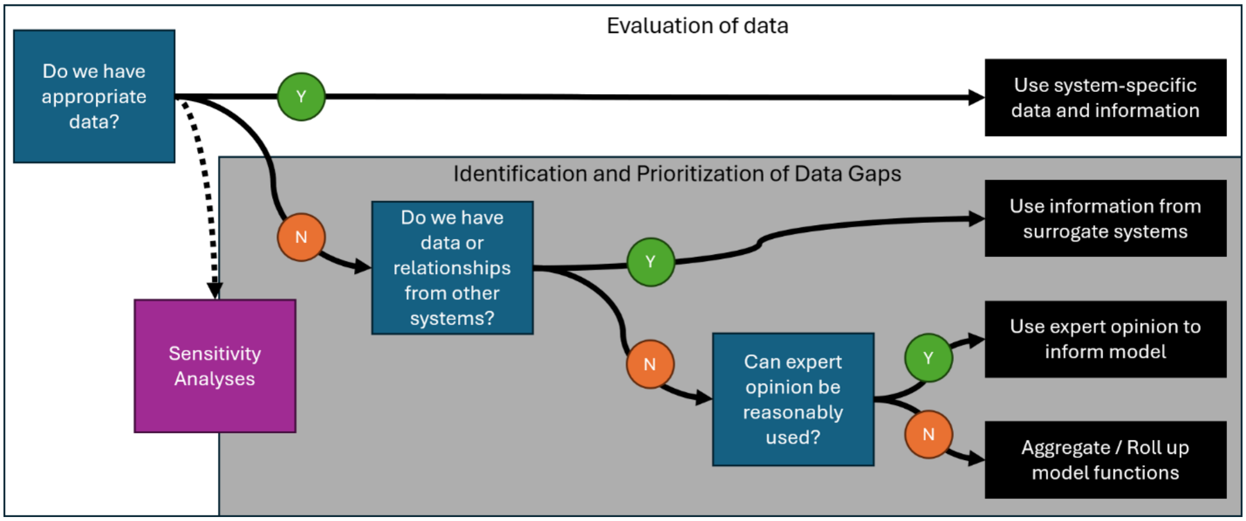

Figure 1. Conceptual diagram showing the process of evaluating data and parameterizing the LCM to support the LFA and management tools.

6.3 Trinity River adaptation of the method

In the Trinity River application, the Hamilton and Murphy (2018) method is adapted to a system where managers primarily control two levers: flow releases and habitat restoration. Important constraints may also occur downstream or in the ocean. The analysis therefore asks whether improving Trinity River flow and habitat can close the adult escapement gap or whether later survival in the Klamath River, estuary, or ocean remains limiting. The LCM links performance at each life-stage transition to candidate hypotheses and management interpretation (Booth et al. 2016; Jorgensen et al. 2021). At the SAB's request, some life stages are represented in greater detail where data support it; otherwise, results are interpreted at broader life-stage scales. Appendix G contains a user guide and related supporting materials describes the graphical user interface, while Appendices A through F and H provide the technical support for model structure, assumptions, data, calibration, expanded results, and uncertainty.

The open-source LCM and graphical user interface are addressed through the LCM framework, transition structure, calibration workflow, scenario tests, and user-guide materials referenced in the appendices. The report summarizes the analytical logic and model application; the detailed code, GUI documentation, and user guide serve as supporting technical products for implementation and future model updates.

6.4 Model Purpose, Appropriate Uses, and Limitations

The LCM is designed to explore why salmon may not be meeting recovery goals and how results change under different assumptions, management actions, or environmental conditions. It can help identify processes that need further study, compare the direction and relative size of responses among scenarios, and determine whether conclusions remain similar when uncertain assumptions are changed. The model is not designed to predict the exact number of salmon in future years, calculate the precise benefit of a specific field action, or prove that one factor caused a bottleneck. Results depend on how the model is structured, the values entered, and the scenarios tested and should therefore be considered together with field observations, uncertainty, and management context.

7. Life Cycle Structure and Model Framework

7.1 Target population and life stages

The Trinity River supports both early- (spring-run) and late-run (fall-run) Chinook salmon (Rupert et al. 2017). Spring-run and fall-run Chinook salmon are not fully reproductively isolated under current regulated and hatchery conditions. Genetic evidence from Trinity River Hatchery returns indicates hybridization, particularly during the spring–fall transition period; however, available public sources do not support a single contemporary basin-wide estimate of introgression (Kinziger et al. 2008). The analysis focuses on natural-origin Trinity River Chinook salmon and represents the major life stages needed to diagnose where survival or production may be insufficient to support adult escapement objectives. At a summary level, these stages include adult return and migration, holding, spawning, egg incubation and redd survival, fry emergence, juvenile rearing, downstream outmigration, nearshore and ocean survival, maturation, and adult return. The purpose of this structure is not to maximize biological detail at every step, but to represent the major transitions needed to test where the adult shortfall is most likely generated and whether those constraints are primarily in-river (Trinity River), downstream (Klamath River), or marine (Jorgensen et al. 2021; Chen et al. 2023). Detailed life-stage definitions and transition descriptions are provided in Appendix A. Detailed model structure and transitions.

The biological scope is intentionally narrower than the full TRRP fisheries mandate. The model represents natural-origin Trinity River Chinook salmon, with spring- and fall-run differences included only where supported by the current structure, such as spring-run adult holding; it does not produce separate run-specific diagnoses. Coho salmon and steelhead share habitats and may respond to many of the same restoration actions, but they are outside this Chinook salmon LFA and require species-specific analyses. Hatchery fish are included only where they affect natural-origin Chinook salmon through spawner allocation or release timing (habitat competition); hatchery production is not a separate modeled population objective. Ocean productivity is represented through age- and condition-specific survival scenarios rather than a mechanistic ocean model. Predation is not isolated as a separate mortality process because Trinity River-specific rates are insufficient; any such effects are embedded within estimated stage survival and remain a monitoring or future scenario-testing need. These boundaries should prevent contextual topics from being interpreted as fully evaluated limiting factors.

7.2 Transition structure

The model follows groups of salmon from adult return through holding, spawning, egg production and incubation, juvenile growth and downstream movement, survival in the estuary and nearshore ocean, ocean survival and maturation, and return to the river (Figure 2). It applies the same equations and input values each time a scenario is run (deterministic) and follows groups of salmon produced in the same brood year through the life cycle (cohort-based). The Phase 1 life cycle diagram shows where each part of the life cycle occurs and how the modeled stages connect. Appendix A defines each modeled transition; Appendix B describes the model assumptions and rules, including the equations and values used. Appendix H details the model input values with the corresponding references, when applicable.

The model implements the Phase 2 Option 3 approach by linking habitat capacity and productivity to life-stage transitions. Scenarios test how habitat, flow, survival, hatchery operations, harvest, and external conditions affect abundance, productivity, spatial structure, and life-history diversity.

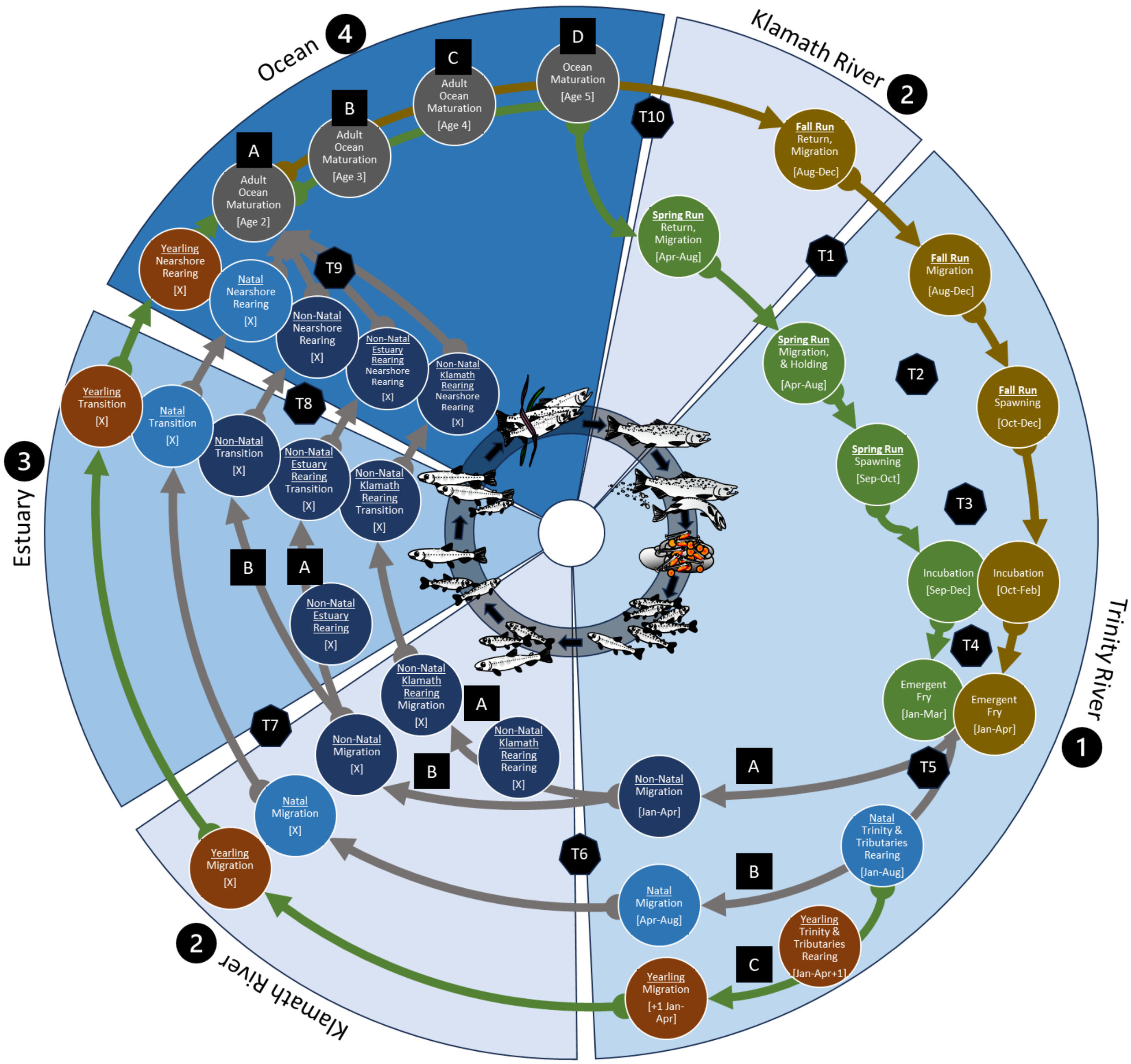

Figure 2. Life cycle diagram (LCD) developed in collaboration with TRRP scientists during Phase 1 of the Trinity River Chinook Limiting Factors Analysis. The LCD was used to develop the life cycle model framework for transitions (T1–T10) between key life stages, life-history variations, and locations, including the Trinity River, Klamath River, estuary, ocean, and return to the Klamath and Trinity rivers. See Appendix A. Detailed model structure and transitions for more information on the LCD and transition structure.

7.3 Spatial structure

The model also includes a simplified spatial structure to distinguish where constraints may arise along the migration corridor. This includes the Trinity River from Lewiston Dam to the Klamath River confluence, the Klamath River from the Trinity confluence to the estuary, the Klamath River estuary and nearshore, and the ocean (Figure 3). Within the Trinity River, the model includes three primary reaches for escapement, spawning, and rearing life stages. These reaches differ in geomorphic structure, rearing capacity, and thermal regimes, which influence juvenile growth opportunities, competition for habitat, and emigration timing. The Trinity River reaches included in the model are:

- **Reach 1:** The upper section of the restoration reach (Lewiston Hatchery to Old Lewiston Bridge / Bucktail, upper 10.9 km).
- **Reach 2:** Rest of the restoration reach (Lewiston/Limekiln/Douglas City/Junction City/North Fork rehab reaches).
- **Reach 3:** Downstream of the restoration reach to the mouth (Big Bar, Del Loma, Salyer Gorge, Willow Creek Valley, Hoopa Valley).

The spatial structure separates Trinity River constraints from downstream and marine constraints and aligns with major monitoring points, including rotary screw traps, adult weirs, and transitions among the Trinity River, Klamath River, estuary, and ocean (Figure 3).

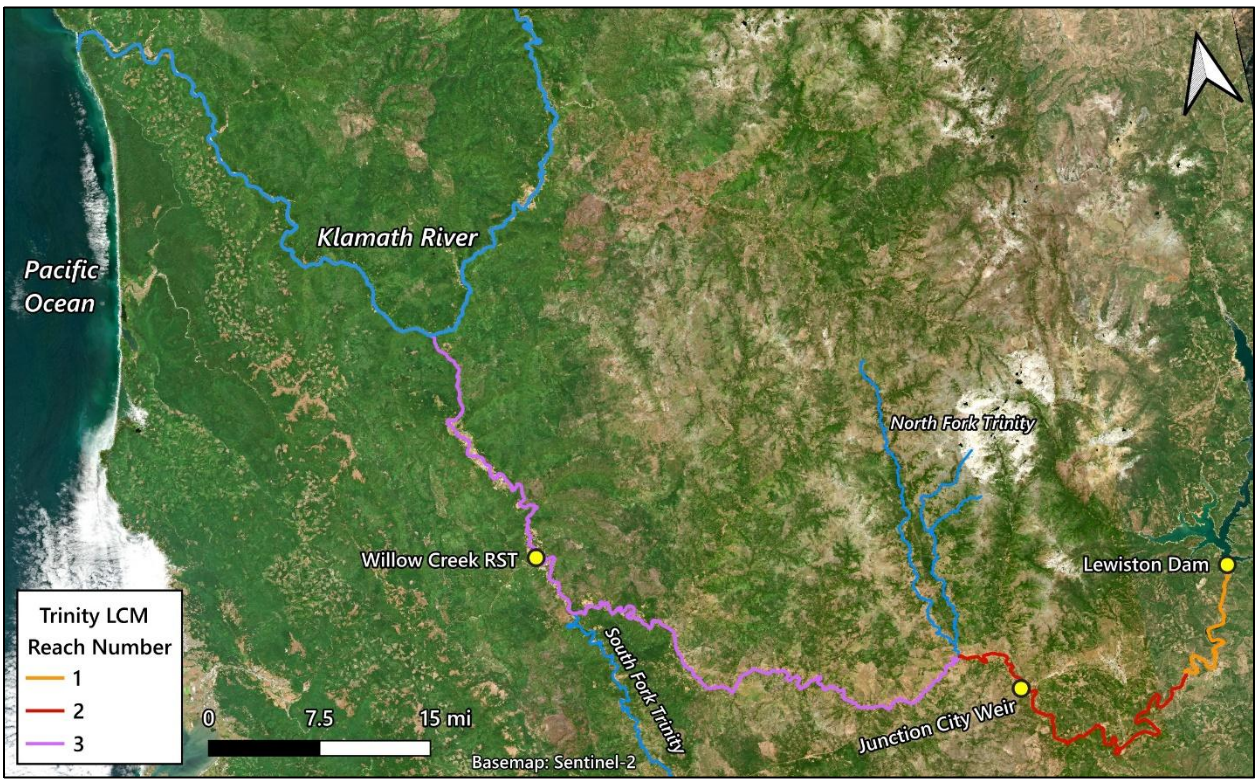

Figure 3. Study area and spatial structure for the Trinity River Chinook salmon life cycle model and limiting factors analysis.

8. Candidate Limiting Factors and Working Hypotheses

At a broad level, the current diagnosis is organized around three competing hypotheses: (1) that spawning and early incubation losses are large enough to depress downstream juvenile production; (2) that juvenile rearing in the Trinity River remains the strongest in-river bottleneck because habitat capacity, growth opportunity, or survival are insufficient; or (3) that downstream (Klamath River) and marine survival are so poor that even substantial freshwater gains would not close the adult escapement gap. These hypotheses differ not only in biological interpretation, but also in management relevance. Spawning and rearing are more directly linked to TRRP flow and habitat actions, whereas downstream (e.g., Klamath River temperature and disease dynamics) and ocean survival are only partly influenceable or largely external. The LFA is intended to test these alternatives against observed versus required performance rather than assume in advance that any single stage explains the adult shortfall. The purpose of comparing these hypotheses is to identify alternative management strategies: emphasize Trinity River habitat improvements if freshwater production is limiting, emphasize partner coordination if downstream or ocean survival dominates, or emphasize monitoring and model refinement where uncertainty prevents a confident diagnosis.

Phase 1 identified candidate limiting factors and organized hypotheses and data requests by life stage, transition, and model geography (Appendix C). Table 1 present hypotheses prioritized for Phase 2 testing.

Several unresolved issues affect how confidently the model can evaluate hypotheses. These include limited information on naturally produced yearlings, rearing habitat below Willow Creek, juvenile survival through the Klamath River, run-specific differences, tributary and hatchery contributions, harvest during adult immigration, and possible overlap between spawning-capacity limits and redd superimposition. Assumptions about fry and parr capacity, yearling habitat, and migration timing also influence model behavior. These uncertainties do not change the overall diagnostic framework, but they limit how precisely some life-stage constraints can be ranked. Appendix B describes model assumptions and unresolved structural issues, and Appendix F summarizes priority data gaps.

The spawning-capacity representation may understate redd superimposition because it assigns spawning habitat without explicitly simulating sequential site reuse after an earlier female dies. Later-arriving females may reuse preferred habitat and disturb existing redds. This risk may be amplified because Lewiston Dam blocks access to upstream spawning habitat, concentrating adults downstream despite their tendency to continue migrating upstream.

9. Data Sources and Inputs

TRRP already has much of the monitoring and modeling foundation needed to evaluate habitat capacity and life-stage performance. S3 and related studies link flow, temperature, habitat quantity and complexity, carrying capacity, growth, survival, and fish production, while the LFA provides a structure for evaluating these relationships across the full life cycle (Cooper Hertel et al. 2022a, 2022b; Plumb et al. 2023; Stantec Consulting Services 2023). However, the quantity and quality of habitat available under different flows remain insufficiently resolved for several life stages. Improving these estimates is central to this LFA because habitat capacity affects whether the model identifies a stage as limiting and whether flow and restoration actions can be evaluated against biological outcomes. Consistent with Merz et al. (2013), abundance at any single life stage is insufficient to determine restoration effectiveness because it reflects cumulative effects across preceding stages.

The principal opportunity is therefore to strengthen how existing monitoring and models are connected to specific LFA hypotheses. For each priority hypothesis, future data collection should quantify how flow and channel conditions affect habitat quantity and quality by life stage, reach, and season, and then link those habitat conditions to carrying capacity, growth or survival, life-stage transition, and adult production. Where feasible, monitoring should provide sufficient spatial, temporal, and treatment contrast to distinguish management effects from background variability and support stronger inference about cause and effect.

TRRP should establish a program-wide data governance framework that links each monitoring activity to explicit management questions or hypotheses, consistent with the emphasis in Merz et al. (2013) on tracking life-stage transitions and environmental relationships rather than collecting data without a defined analytical purpose. Effective data stewardship means data is collected, stored, and maintained in a manner that allows for high-quality, repeatable scientific analyses, with standardized protocols that ensure accurate and precise processes across all data users, especially when those users span different organizations. This requires a definitive repository for finalized data and shared access across organizations. It also requires metadata documenting protocol changes, un-sampled periods, or other issues that could affect summaries and analyses. Clear communication whenever study plans or designs change is equally essential, so data can be analyzed consistently through time despite those changes. Where practical, TRRP should adapt proven regional approaches, such as the Healthy Rivers and Landscapes science framework, which includes coordinated hypotheses, common metrics, and interoperable datasets, rather than building new systems independently. Doing so would increase transparency, ease analysis, and make existing monitoring investments more useful for adaptive management.

Data used to parameterize the Trinity River Chinook salmon LCM were identified through a structured data requirements process developed in close coordination with TRRP scientists and the TAG (Appendix C. Data sources and input requirements). The data request framework was organized around key life stages and transitions in the Chinook salmon life cycle, with associated hypotheses and potential limiting factors developed collaboratively during Phase 1 of the analysis. This process emphasized Trinity River-specific empirical datasets wherever possible, including long-term monitoring of adult returns, redd surveys, carcass surveys, and outmigrant abundance estimates from rotary screw traps, which collectively provide the primary basis for informing abundance, timing, life-history expression, and survival across major freshwater stages.

Support for each rule, parameter, and conclusion is identified in the supporting appendices as Trinity River-specific data, surrogate-system data, published literature or mechanistic relationships, or expert-derived values. Trinity River-specific data were used first; surrogate and published information bounded plausible values when local data were insufficient; and expert-derived values were used only where empirical support remained incomplete. Appendices B, D, and H document the sources, assumptions, calibration, and sensitivity of parameter values, while Table 3 summarizes confidence in the resulting interpretations.

Priority data collection should be hypothesis-specific and address several important limitations. S3 provides a useful analytical framework, but available information indicates that it may substantially overestimate some habitat; its habitat and capacity estimates should therefore be independently validated against observed habitat use, fish density, growth, condition, and survival. Rotary screw trap estimates should be calibrated for differences in capture susceptibility among life stages and fish sizes and expanded or supplemented to account for production from tributaries not represented at the mainstem traps. Updated reach-specific studies are also needed because spawning and incubation habitat quality has not been comprehensively evaluated for many years. These studies should quantify spawning capacity, substrate suitability, fine sediment, hyporheic conditions, redd reuse and superimposition, and survival from egg to fry. Together with improved estimates of Trinity River origin survival through the Klamath River and estuary, these data would reduce uncertainty in the LFA hypotheses most likely to affect management decisions (Merz et al. 2013; Cooper Hertel et al. 2022a; Plumb et al. 2023; Stantec Consulting Services 2023).

10. Calibration, Tuning, and Model Review

Calibration was used to establish a plausible baseline for testing the Phase 2 hypotheses (H_1–H_{20}; Table 1), not to prove that the model is correct. Parameters and assumptions were adjusted so model outputs reasonably matched three observed measures: natural-origin adult escapement to the Trinity River, age-0 natural-origin outmigrant abundance at the Willow Creek rotary screw trap, and brood-year smolt-to-adult return rates. These checkpoints support hypotheses concerning systemwide limitation (H_1), juvenile rearing and production (H_9–H_{11} and H_{18}), downstream and early marine survival (H_{12}–H_{13}), ocean survival and harvest (H_{14}–H_{15}), and cross-stage effects (H_{16}–H_{17} and H_{20}). No single period contains complete adult, juvenile, and marine data, so the calibration checkpoints span different periods and may influence the apparent balance between freshwater and marine limitation. Calibration shows that the model can reproduce selected observations; it does not validate the model against independent data. Different combinations of model parameters or assumptions may reproduce the same calibration checkpoints while implying different bottlenecks (equifinality). The calibrated model is therefore one plausible representation for comparing hypotheses and scenarios, not a tool for precise forecasting or unique causal attribution. Appendix D retains the calibration values, adjustments, data sources, tuning rationale, supporting citations, and sensitivity analyses used to evaluate whether conclusions remain stable under alternative assumptions.

Juvenile outmigration size and timing were not fully calibrated. Willow Creek length data combined hatchery- and natural-origin fish and therefore could not be used to calibrate natural-origin outmigration size, and the timing-calibration step was not completed. Appendix B documents the associated model assumptions and limitations.

11. Phase 2 Diagnostic Results

The Phase 2 diagnosis evaluates which constraints most affect Trinity River adult escapement under the current model structure and assumptions. The analysis is organized across six life-stage blocks: adult immigration and holding, spawning, incubation and emergence, juvenile rearing, outmigration through the estuary and early marine period, and ocean maturation and survival. Table 1 links hypotheses to transitions and tests, Table 2 summarizes the 27 planned tests by life stage, and Table 3 links each test to its finding, classification, confidence rating, and supporting figures in Appendix E.

For each completed test, the calibrated model was held at baseline conditions while one process, capacity, or related group of factors was changed. Differences in the direction and relative magnitude of modeled escapement were used to identify sensitivities and plausible limiting stages. These results are conditional comparisons, not forecasts of future abundance or estimates of the effect of a specific field action. The nested limiting-factor scenario combines selected constraints sequentially as a synthesis and is not counted as an additional test; pending tests remain in the framework but are not interpreted as completed results. Appendices B, D and H document assumptions, evidence sources, calibration, and sensitivity, and Appendix E provides expanded results.

The analysis tested hypotheses developed with TRRP and SAB (Table 1). After identifying a likely constraint, the model relaxed it to determine what became limiting next. Biological effect, uncertainty, evidence source, and degree of TRRP influence informed prioritization.

The rationale linking tests to conclusions is consistent across life stages. Each hypothesis identifies a candidate process; its diagnostic test changes that process relative to calibrated baseline conditions and evaluates the direction and relative magnitude of the response in adult escapement or relevant carryover traits. A factor is classified as primary when plausible improvement closes much of the recovery gap or its persistence prevents the target from being reached; compounding when it materially affects production or survival but is insufficient alone; non-limiting when plausible changes produce little meaningful response under baseline conditions; and episodic when effects emerge mainly under extreme conditions or narrow time windows. The nested scenario sequentially relaxes supported constraints to determine what becomes limiting next, whereas sensitivity analyses test whether conclusions remain stable when uncertain parameters or assumptions vary. Conclusions therefore reflect the combined hypothesis, diagnostic response, nested sequence, evidence basis, and sensitivity, not the output of any single run.

Table 1. Hypotheses evaluated in the Trinity River Chinook salmon limiting factors analysis, with corresponding life-stage transitions and diagnostic tests. See Appendix A. Detailed model structure and transitions for more detail on transitions (T).

ID	Life Stage	Transition	Related Tests	Hypothesis
H_1	Systemwide	All	Multiple	Adult returns appear more strongly limited by downstream-to-ocean survival and harvest than by Trinity freshwater production alone.
H_2	Adult immigration	T10 → T2	Adult Imm. T1–T4	Immigration survival limits escapement but is not sufficient alone to explain the recovery gap.
H_3	Adult holding	T10 → T2	Adult Imm. T2	Holding habitat limits escapement only under specific conditions and is otherwise non-limiting.
H_4	Spawning	T2 → T3	Adult Imm. T3; Spawning T3	Spawning habitat capacity is a compounding constraint that becomes limiting only under substantial reductions.
H_5	Incubation	T3 → T4	Incub. T1–T6	Egg-to-fry survival influences production but is not a primary limiting stage under typical conditions.
H_6	Incubation	T3 → T4	Incub. T2	Coarse substrate limits redd construction, especially for smaller females.
H_7	Incubation	T3 → T4	Incub. T3	Fine sediment reduces survival above threshold levels and acts as a conditional constraint.
H_8	Incubation	T3 → T4	Incub. T4–T5	Episodic stressors affect survival primarily under extreme conditions.
H_9	Rearing	T4 → T5	Rearing T1–T5	Juvenile rearing capacity and growth are the strongest direct Trinity-managed constraints, but their adult-return effects depend on downstream and marine survival.
H_{10}	Rearing	T4 → T5	Rearing T1, T4	Increasing juvenile production alone cannot achieve recovery if downstream survival remains low.

ID	Life Stage	Transition	Related Tests	Hypothesis
H_{11}	Rearing	T4 → T5	Rearing T2–T3; T6	Trade-offs between size and abundance influence downstream survival and adult returns, and are mitigated by flows, habitat, and outmigration timing.
H_{12}	Outmigration	T5 → T9	Outmig. T1, T2	Juvenile outmigration mortality through the Klamath and estuary limits escapement.
H_{13}	Outmigration	T5 → T9	Outmig. T1; Ocean T3	Juvenile size at outmigration strongly influences downstream and early marine survival.
H_{14}	Ocean	T9 → T10	Ocean T1	Ocean harvest is interpreted as a primary limiting factor under the scenarios tested.
H_{15}	Ocean	T9 → T10	Ocean T2–T3	Early marine and ocean-entry conditions appear to be dominant survival drivers.
H_{16}	Cross-stage	Multiple	Multiple	Limitation reflects carryover effects across life stages rather than isolated bottlenecks.
H_{17}	Cross-stage	Multiple	Multiple	Early-stage processes influence size, condition, and later survival and reproduction.
H_{18}	Outmigration	T5 → T9	Rearing T6	Improvements in size and timing persist through downstream survival.
H_{19}	Outmigration	T5 → T9	Outmig. T3	Increased production can offset downstream mortality under limiting conditions.
H_{20}	Systemwide	All	Ocean T4	Coordinated improvements across life stages can achieve recovery targets.

Table 2. Life stages, transitions, and number of diagnostic tests performed. Life stages and transitions are described in Appendix A. Detailed model structure and transitions. Assumptions and rules are provided in Appendix B. Assumptions and rules and supporting figures and tables for LFA results are provided in Appendix E. Expanded LFA results.

Life Stage	Short Name	Transition	Number of LFA Tests
Adult immigration and holding	Adult Immigration	T10 → T2	4
Spawning	Spawning	T2 → T3	4
Incubation and emergence	Incubation	T3 → T4	6
Juvenile rearing	Rearing	T4 → T5	6
Outmigration, estuary, and early marine survival	Outmigration	T5 → T9	3
Ocean maturation and survival	Ocean	T9 → T10	4
Total			**27**

Table 3. Test-level synopsis of the 27 diagnostic tests. Class: P = primary, C = compounding, N = non-limiting. Control: In = directly manageable by the Trinity River Restoration Program, Partial = influenceable but not controllable, External = mostly outside Trinity management. Basis: D = data/model-driven, EI = relied substantially on expert-derived values or assumptions. Figure numbers provide references for figures in Appendix E.

Life Stage	Test	Finding	Class	Control	Conf.	Figure Number (Appx. E)
Adult immigration	Adult Imm. T1	Improved Klamath–Trinity immigration and routing survival increased escapement but did not achieve the recovery target alone.	C	Partial	Med.	1-2

Life Stage	Test	Finding	Class	Control	Conf.	Figure Number (Appx. E)
Adult immigration	Adult Imm. T2	Spring-run holding habitat was non-limiting under current conditions; effects appeared mainly under no-harvest or higher-escapement scenarios.	N	In	Low–Med.	3-4
Adult immigration	Adult Imm. T3	Spawning capacity was compounding and became more limiting under large reductions; hatchery-origin spawner allocation had small effects.	C	In	Med.	5-11
Adult immigration	Adult Imm. T4	Best-plausible immigration improved escapement but did not meet the target; rearing capacity was the most sensitive Trinity-managed capacity.	C	In/Partial	Med.	12-15
Spawning	Spawning T1	Mirrors Adult Imm. T1: improved migration survival increased returns but did not resolve the spawner shortfall.	C	Partial	Med.	1-2
Spawning	Spawning T2	Mirrors Adult Imm. T2: spring-run holding habitat did not constrain total adult escapement under current conditions.	N	In	Low–Med.	3-4
Spawning	Spawning T3	Mirrors Adult Imm. T3: spawning capacity was compounding and could become primary under large reductions.	C	In	Med.	5-11
Spawning	Spawning T4	Mirrors Adult Imm. T4: remaining limitation shifted toward Trinity-managed habitat, especially rearing capacity.	C	In/Partial	Med.	12-15
Incubation	Incub. T1	Best combined incubation survival increased fry production and escapement but did not reach the recovery target alone.	C	In	Med.	16-17
Incubation	Incub. T2	Coarse gravel became limiting by reducing female redd-construction success; interpretation is limited by reach-scale substrate data gaps.	C	In/Partial	Low–Med.	18-19
Incubation	Incub. T3	Fine sediment had little effect at moderate levels but substantially reduced escapement at high to extreme levels.	C	In/Partial	Low–Med.	20-21
Incubation	Incub. T4	Hydrologic disturbance was non-limiting under stable to minor conditions but episodic under moderate to extreme disturbance.	N/epis.	Partial	Med.	22
Incubation	Incub. T5	Maternal thiamine deficiency was generally non-limiting except under moderate to severe deficiency.	N/epis.	External	Low–Med.	23-26

Life Stage	Test	Finding	Class	Control	Conf.	Figure Number (Appx. E)
Incubation	Incub. T6	Best plausible incubation increased juvenile outmigrant abundance and escapement but remained insufficient to reach the target alone.	C	In	Med.	27-29
Rearing	Rearing T1	Rearing capacity controlled emigration timing and size; large capacity reductions substantially reduced escapement.	C	In	Med–High	30-36
Rearing	Rearing T2	Sustained early food increased escapement but did not reach the target; shorter food-limited periods had little effect.	C	In/Partial	Med.	37-38
Rearing	Rearing T3	Cool or optimal temperatures improved production; rapid warming reduced escapement and highlighted size-survival tradeoffs.	C	In/Partial	Med.	39-41
Rearing	Rearing T4	Baseline Trinity production exceeded targets when downstream and ocean survival were favorable, indicating primary systemwide downstream and marine constraints rather than insufficient Trinity production alone.	P	Partial/Ext.	Med–High	42-43
Rearing	Rearing T5	Hatchery release timing changed natural-origin migrant size distribution but had little effect on long-term escapement.	N	In	Low	44-46
Rearing	Rearing T6	Flow and habitat can influence emigration size and timing, which can influence downstream survival and escapement.	C	In	Low	47-50
Outmigration	Outmig. T1	Large losses occurred from the Trinity through Klamath, estuary, and ocean entry; larger fish survived better.	C/P	Partial	Med.	51-52
Outmigration	Outmig. T2	Klamath flow, temperature, and disease scenarios produced wide escapement differences and strong episodic effects.	C/epis.	Partial	Med.	53-54
Outmigration	Outmig. T3	Test whether increased Trinity production can offset downstream mortality under limiting conditions (Untestable with final model structure).	N/A	N/A	N/A	N/A
Ocean	Ocean T1	Ocean harvest was primary; reducing ocean harvest produced large escapement increases and could exceed the target.	P	External	Med–High	55-56
Ocean	Ocean T2	Favorable early marine and ocean-entry conditions substantially	P	External	High	57-58

Life Stage	Test	Finding	Class	Control	Conf.	Figure Number (Appx. E)
		increased escapement; highest-probability systemwide factor.				
Ocean	Ocean T3	Freshwater production to ocean entry showed major attrition, especially through the Klamath corridor, with strong size-dependent survival.	C/P	Partial	Med.	59-60
Ocean	Ocean T4	Nested limiting-factor scenario shows that coordinated improvements across ocean, Klamath River, and Trinity River conditions increased modeled escapement from baseline to 68,035 adults.	P/C	Mixed	Med.	61

11.1 Nested limiting factors scenario

The tuned and calibrated Trinity LCM provides a baseline estimate of Trinity River pre-spawn adult escapement under existing modeled conditions. Across the baseline simulation period, mean annual Trinity River pre-spawn escapement was 9,581 adults. This value represents model-average escapement for the baseline scenario and serves as the reference point for evaluating the relative influence of successive limiting factors (Figure 4).

The nested scenario indicates that the combined ocean changes tested produced the largest modeled escapement gain in the sequence. Reducing harvest by approximately 10 to 20% for each age class and increasing ocean survival by 3% for ages 3, 4, and 5 increased modeled mean Trinity River pre-spawn escapement from 9,581 to 37,520 adults (Figure 4). TRRP restoration remains essential because it improves the juvenile production, size, timing, and condition needed to translate favorable downstream and ocean conditions into stronger adult returns. The parameter changes represent plausible, management-relevant improvements supported by observed ranges, literature, sensitivity testing, or structured expert-derived values; they are not predictions that any single action would achieve those values. Appendix B and H document the source and rationale for each value. The nested sequence is intended to reveal shifting constraints, not prescribe a restoration package.

After accounting for ocean effects, Klamath River conditions were the next most influential constraint. Eliminating disease-related mortality and maintaining nominal Klamath River temperatures further increased modeled mean Trinity pre-spawn escapement to 53,908 adults (Figure 4).

Finally, the nested results indicate that Trinity River conditions continue to constrain adult production even after ocean and Klamath River constraints are reduced. Increasing weekly base rearing survival from 0.95 to 0.96, adding 4,000 m^2 of rearing habitat to each reach under each flow condition, and slightly reducing rearing temperatures in all three reaches increased modeled mean Trinity River pre-spawn escapement to 68,035 adults (Figure 4). The Trinity increment is therefore best interpreted as the modeled benefit of improving life-stage conditions TRRP can most directly affect, not as a complete measure of program value.

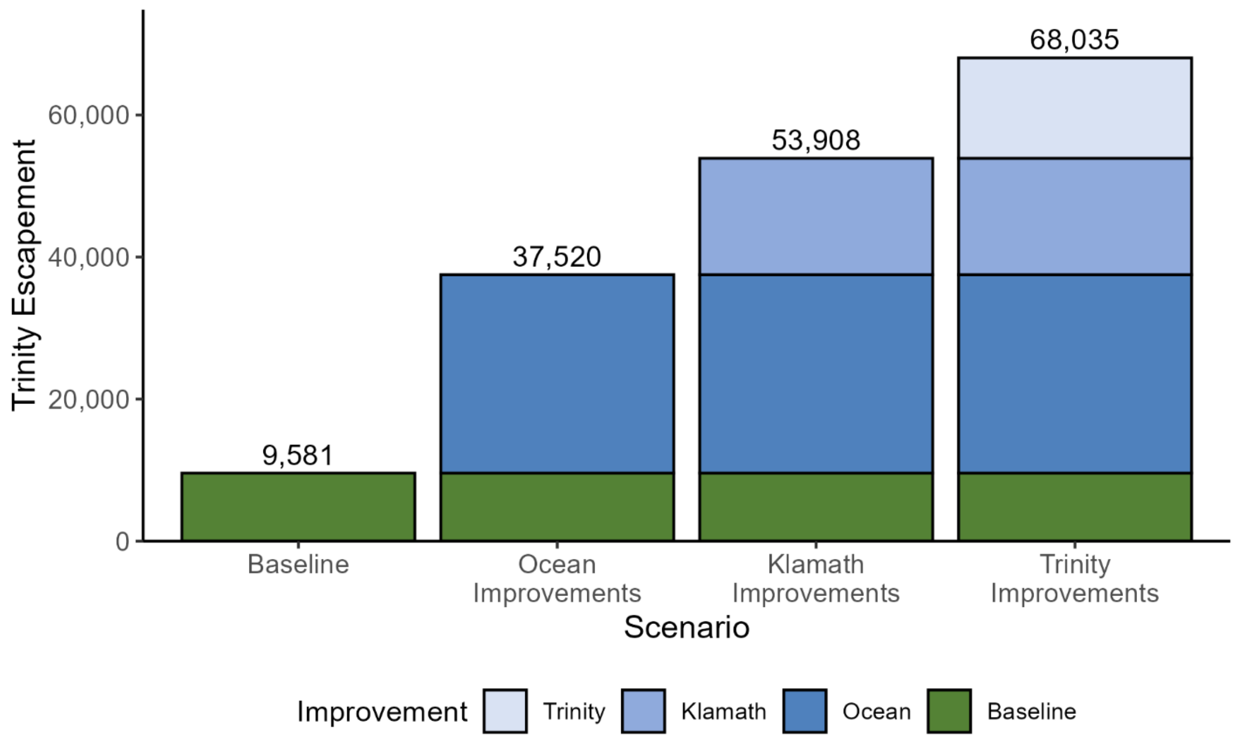

Figure 4. Modeled mean Trinity River pre-spawn adult escapement under nested limiting-factor scenarios. Bars show cumulative changes from baseline conditions (green), ocean improvements (dark blue), Klamath River improvements (blue), and Trinity River improvements (light blue). Baseline escapement represents mean annual pre-spawn escapement across the baseline simulation period.

The nested scenarios show constraints operating at multiple spatial scales: ocean conditions produced the largest modeled escapement gain, followed by Klamath River disease and temperature improvements and additional gains from Trinity River rearing habitat, survival, and temperature. These outputs are diagnostic comparisons, not forecasts; their apparent numerical precision reflects the specific inputs and assumptions used. The results should therefore be interpreted by the direction and relative magnitude of responses among scenarios rather than as precise predictions of future escapement. Subsequent sections present diagnostics by life-stage block.

When a result appears counterintuitive, users should first verify the baseline and changed inputs, then check whether harvest thresholds, density dependence, spatial redistribution, capacity limits, or size- and timing-dependent survival changed elsewhere in the life cycle. Compare intermediate abundance, size, timing, and reach outputs, not only final escapement, and rerun one change at a time. For example, reduced habitat can appear beneficial if fish redistribute to a reach with higher modeled survival; this is a structural diagnostic, not evidence that habitat loss is beneficial.

11.2 Adult immigration and holding

This section evaluates hypotheses H_2 through H_4 related to adult immigration, holding, and spawning capacity (Table 1). Results for Adult Imm. T1 through T4, including classifications, confidence ratings, and supporting figures, are summarized in Table 3 and Appendix E, Figures 1 through 15.

The first question is whether adults reach the Trinity River and hold under conditions that reduce survival before spawning. Relevant information includes lower Klamath and Trinity river temperature and disease records, flow conditions, migration timing, and historical mortality events (FitzGerald and Martin 2022; Van Wert et al. 2023). These data help evaluate whether low flow, warm temperature, crowding, or disease exposure create meaningful risk (Keefer et al. 2025). In the diagnostics, improving immigration and routing survival at the Klamath–Trinity confluence increased simulated escapement by roughly two to two-and-a-half times, but escapement still leveled off near 27,000 adults. Even complete immigration survival produced only about half of the recovery target (Table 3 Adult Imm. T1; Appendix E. Expanded LFA results, Figures 1 through 2). Immigration conditions are therefore a compounding limiting factor: important, but not sufficient on their own to close the recovery gap.

Holding habitat applies only to spring-run Chinook salmon. They are the only run type in this analysis with clear holding behavior, typically holding for a month or more while completing maturation and awaiting appropriate spawning conditions (Campbell and Moyle 1992; FitzGerald and Martin 2022; Naylor et al. 2025). Thus, only the spring-run component is directly affected by holding behavior or holding-capacity assumptions. Doubling or tripling holding capacity had little effect under baseline harvest. A response appeared only when in-river harvest was removed because harvest scales dynamically with population size, a key part of model calibration, keeping the population below holding habitat capacity. Once harvest was removed, the population grew enough to reach holding habitat capacity, and additional holding habitat then increased escapement by about thirty percent relative to baseline (Table 3 Adult Imm. T2; Appendix E. Expanded LFA results, Figure 3 through 4). Because spring-run fish are currently a smaller share of total escapement, holding habitat is classified as non-limiting under current conditions. It could become more important under higher-escapement or reduced-harvest scenarios, but holding capacity remains poorly constrained by data and depends on assumptions about holding area, density, spacing, and temperature (Campbell and Moyle 1992; FitzGerald and Martin 2022). This classification is conditional on current spring-run abundance and baseline harvest assumptions and should not be read as a conclusion that holding habitat has low ecological value.

Adult Immigration Test 3 evaluated whether spawning habitat limits escapement after accounting for age structure, sex ratio, and hatchery contribution. With harvest removed, escapement declined as spawning capacity was reduced. The response was non-linear: 10 to 25% reductions lowered escapement by roughly 5 to 15%, while 50 to 75% reductions lowered escapement by roughly 35 to 50% (Table 3 Adult Imm. T3; Appendix E. Expanded LFA results, Figures 5–11). Moving hatchery-origin spawners downstream produced only small increases in natural-origin escapement. Figures 5 through 11 are the key cross-references for evaluating the spawning-capacity and hatchery-origin spawner-allocation results. These results suggest spawning habitat is a compounding factor that can become primary only under large capacity reductions (Groves et al. 2013; Maunder 1997). The hatchery-origin spawner distribution result should be treated cautiously because the test is a coarse representation of density effects, redd superimposition, behavioral interactions, and fine-scale habitat competition (Geist and Dauble 1998; Harrison et al. 2019; McHugh and Budy 2004; Riebe et al. 2014).

Accordingly, the spawning-capacity result should be interpreted cautiously. The model does not fully represent sequential female arrival, post-spawn site reuse, or behaviorally driven concentration below Lewiston Dam and may therefore underestimate redd superimposition and associated egg loss (Maunder 1997; Dudley 2019).

Finally, the location of the bottleneck was examined under best-plausible immigration conditions. Applying the best plausible Klamath and Trinity immigration conditions increased simulated escapement by about 250% relative to baseline but still failed to meet the recovery target, and the response weakened markedly as habitat capacities were lowered; reducing capacities to half of baseline reduced the gain to about 80% (Table 3 Adult Imm. T4; Appendix E. Expanded LFA results, Figure 12 through 15). When capacities were reduced individually, simulated escapement was most sensitive to reductions in juvenile rearing capacity. These results indicate that immigration conditions are an important compounding limiting factor, that improving immigration alone is insufficient, and that Trinity-managed habitat, especially rearing capacity, becomes increasingly influential as immigration conditions improve.

11.3 Spawning

This section evaluates H_4, spawning capacity (Table 1). Because the four spawning diagnostics duplicate Adult Immigration Tests 1 through 4, they are summarized rather than repeated. Immigration and routing losses were compounding; holding habitat was non-limiting under baseline conditions; spawning capacity became important only under large reductions; and under best-plausible upstream conditions, rearing capacity produced the strongest remaining Trinity-managed habitat signal (Table 3; Appendix E, Figures 1 through 15).

A compounding classification does not mean spawning habitat is unimportant. It means that spawning improvements are most likely to increase adult returns when they are paired with survival gains in later life stages. One counterintuitive spawning-capacity result illustrates how the model handles spatial redistribution (Appendix E, Expanded LFA results, Figure 5). When spawning habitat is reduced in Reach 1, modeled adult escapement can increase because spawners are redistributed into available habitat in Reach 2. In the model, Reach 2 has higher egg-to-fry survival and is closer to the point of emigration, meaning emigrants face less cumulative mortality across the rearing period. This result only appears when harvest is at baseline conditions. Under no-harvest conditions, the spawning capacity is constraining the population, and escapement decreases as expected when Reach 1 capacity is reduced. This result should not be interpreted to mean that reducing spawning habitat is beneficial; it illustrates how spawning location, habitat quality, harvest dynamics, and proximity to emigration interact in the model.

Modeled redistribution reflects available capacity rather than explicit adult spawning behavior. Field-based estimates of arrival timing, redd reuse, superimposition, and spawning distribution are needed before concluding that adults would redistribute without additional egg loss (Groves et al. 2013; Dudley 2019).

Model spawning capacity was derived from S3 habitat estimates matched to representative spawning-season flows and allocated among the three reaches using a consistent 10/40/50 percent distribution. Total capacity was then tuned while retaining that spatial distribution; Appendix B documents the derivation and tuning assumptions.

11.4 Egg incubation and fry emergence

This section evaluates hypotheses H_5 through H_8 related to spawning-to-emergence processes (Table 1). Six tests evaluated gravel size, fine sediment, hydrologic disturbance, thiamine deficiency, and best-plausible incubation conditions (Tables 2 through 4; Appendix E, Figures 16 through 29). Gravel size affects redd construction, whereas fine sediment affects egg incubation, hyporheic exchange, egg-pocket habitat, and fry emergence (Kondolf and Wolman 1993; McHugh and Budy 2004; Riebe et al. 2014; Tonina and Buffington 2009; Sear et al. 2017; Harrison et al. 2019; Merz et al. 2019). The tests also considered temperature, scour or dewatering, thiamine deficiency, and flow stability (Merz et al. 2004; Jaeger et al. 2024). Where Trinity River-specific estimates were limited, the analysis used expert-derived values and mechanistic expectations as interim assumptions. Best-plausible incubation conditions increased emergent fry from about 8.8 million to 28 million and escapement to roughly two to two-and-a-half times baseline but did not reach the recovery target (Table 3, Incub. T1; Appendix E, Figures 16 through 17). Incubation is therefore classified as compounding rather than primary and remains data-poor.

Specific spawning-to-emergence stressors were tested separately. Gravel size had little effect at 6 cm but sharply reduced escapement at >7 cm because coarse substrate was assumed to limit redd construction, especially for smaller or younger females (Table 3 Incub. T2; Appendix E. Expanded LFA results, Figures 18 through 19; Kondolf and Wolman 1993; Riebe et al. 2014; Merz et al. 2024). This result should be interpreted as a gravel-size and fish-size interaction rather than a simple substrate effect. Fine sediment had little effect at moderate levels but reduced escapement at concentrations above 15%, consistent with reduced egg-to-fry and emergence survival rather than redd-construction failure (Table 3 Incub. T3; Appendix E. Expanded LFA results, Figures 20 through 21; Tappel and Bjornn 1983). Hydrologic disturbance had little effect under stable or minor conditions but reduced escapement under moderate to extreme disturbance (Table 3 Incub. T4; Appendix E. Expanded LFA results, Figure 22). Thiamine deficiency had little effect under no or mild deficiency but reduced escapement under moderate to severe deficiency; a no-harvest diagnostic confirmed the expected decline after removing harvest-threshold artifacts (Table 3Incub. T5; Appendix E. Expanded LFA results, Figures 23 through 26). Overall, these are compounding or episodic factors, not primary limits under typical conditions. These threshold responses reflect how the model represents substrate suitability and emergence survival, so they should be interpreted as diagnostic sensitivity tests rather than precise field thresholds.

A final integrative test indicated that applying the best plausible incubation and emergence conditions increased the number of juvenile outmigrants leaving the Trinity River from fewer than one million to about fifteen million and increased escapement two and a half times, from roughly ten thousand to twenty-five thousand adults, but did not by itself reach the recovery target (Table 3 Incub. T6; Appendix E. Expanded LFA results, Figures 27 through 29). These results support the interpretation that the spawning-to-emergence sequence is not a primary limiting life stage under the scenarios tested, although it is affected by compounding factors that can be important in particular years or reaches. This stage remains data-poor, and several diagnostics relied on generalized, reach-scale assumptions in the absence of spatially explicit data on spawning gravel suitability, fine sediment, and egg-to-fry survival.

11.5 Juvenile rearing

This section evaluates hypotheses H_9 through H_{11} and H_{18} related to juvenile rearing capacity and growth (Tables 1 through 4; Appendix E, Figures 30 through 50). Juvenile rearing is central because TRRP flow and habitat actions directly affect habitat quantity, growth opportunity, temperature exposure, density dependence, and the size and timing of juvenile outmigration (Booth et al. 2016; Jorgensen et al. 2021; Perry et al. 2018b; Sellheim et al. 2025). Trinity River-specific information on naturally produced yearlings remains limited, so the diagnosis emphasizes subyearlings and uses simplified yearling assumptions (Weitkamp et al. 2015; Apgar et al. 2021; Lamperth et al. 2025). Model results indicate that reduced rearing capacity lowers escapement and shifts emigration toward fry and small parr below 55 mm; Reach 1 exceeded capacity in all scenarios, while Reaches 2 and 3 reached capacity earlier as capacity declined. These results identify juvenile rearing as the strongest direct TRRP-managed habitat lever and a Tier 1 priority for management and data refinement, but not necessarily the primary systemwide bottleneck. The estimated effect remains uncertain because rearing habitat quantity and quality, density dependence, growth, survival, and flow–habitat relationships are incompletely resolved, and because abundance–size tradeoffs can influence later survival (Plumb et al. 2025; Sturrock et al. 2026).

Rearing-capacity estimates are uncertain because S3 reported capacity as numbers of fry or parr rather than habitat area and was considered to overestimate available capacity (Pers. Comm. TRRP members). Model values therefore relied partly on expert-derived values; Appendix B documents the derivation, assumptions, and parameter values. Because flow and channel bathymetry jointly determine when, where, and how much habitat is available and how salmon use the habitat, TRRP should continue quantifying flow–habitat relationships to estimate the quantity and quality of habitat available to each life stage across reaches and seasons (Pasternack et al. 2004; Pasternack and Brown 2013; Perry et al. 2018b; McNeely et al. 2026).

Food availability, temperature, and hatchery releases were also tested. Persistently sufficient food during the first fifteen weeks of rearing increased long-term escapement relative to baseline, though not to the recovery target, while shorter food-limited periods had little effect; food availability is therefore compounding rather than primary (Table 3 Rearing T2; Appendix E. Expanded LFA results). Prolonged cool and optimal temperatures increased escapement and produced more outmigrants, but density dependence and timing effects shifted the population toward smaller, earlier migrants with lower individual survival; rapid warming sharply reduced escapement (Table 3 Rearing T3; Appendix E. Expanded LFA results). Hatchery release timing had little effect on escapement but altered the size distribution of natural-origin migrants, and this result should be revisited with a realistic release schedule (Table 3 Rearing T5; Appendix E. Expanded LFA results). Habitat saturation and food availability are represented separately in the model: saturation is based on available habitat, fish abundance, and fish size, whereas food availability affects growth independently. The model does not dynamically link food limitation to increasing habitat saturation because that relationship is complex and was not included in this version. Accordingly, the food and habitat tests diagnose sensitivity to separate assumptions and do not resolve how their interaction may affect rearing limitation in the river.

These results suggest that early flow actions should not be evaluated by juvenile abundance alone. If higher early flows increase outmigrant abundance without improving rearing habitat quality, growth opportunity, or downstream survival conditions, the result could be more juvenile outmigrants but little or no improvement in smolt-to-adult return rate. The model does not uniformly reward rapid juvenile emigration: earlier departure can increase abundance leaving the Trinity River but may reduce size and subsequent survival, whereas additional rearing can produce fewer, larger fish with higher per-fish survival.

Rearing Test 4 evaluated whether Trinity River juvenile production is the primary bottleneck or whether adult returns are mainly limited after fish leave the Trinity River. Improving survival across the Klamath corridor, estuary, ocean entry, and later ocean stages, while holding Trinity River conditions at baseline, produced simulated escapement above the recovery target even with 10 to 50% reductions in habitat capacity (Table 3, Rearing T4; Appendix E, Expanded LFA results). This diagnostic result indicates that downstream and marine survival are primary systemwide constraints under the scenarios tested. It does not diminish the importance of Trinity River rearing, which remains the strongest direct TRRP-managed lever because juvenile abundance, size, timing, condition, and life-history diversity influence downstream survival.

Rearing Test 6 evaluated whether Trinity River rearing improvements that change juvenile size and migration timing could persist through downstream selective mortality and increase adult returns. Alternative flow and habitat scenarios produced different combinations of emigrant abundance, size, and timing. In the model, scenarios with many small emigrants tended to have lower downstream survival, whereas scenarios with fewer but larger emigrants tended to have higher per-fish survival through the Klamath River, estuary, and ocean-entry stages (Table 3 Rearing T6; Appendix E. Expanded LFA results). These results caution against relying on juvenile abundance alone as a success metric and support maintaining a diverse portfolio of juvenile life histories rather than optimizing for one migrant type.

11.6 Outmigration, estuary, and early marine survival

This section evaluates hypotheses H_{12}, H_{13}, and H_{19} (Tables 1 through 4). This life stage links juvenile size, timing, and condition in the Trinity River to survival through the lower Trinity River, Klamath River, estuary, nearshore, and early ocean period. The diagnosis asks whether fish die during migration or leave the Trinity River at sizes, times, or conditions that increase downstream risk. Trinity River flows may affect this pathway through the quantity and quality of water entering the lower Klamath River, including temperature and other conditions affecting emigrating juveniles (Perry et al. 2018a, 2018b; Plumb et al. 2025; Bartholomew et al. 2023).

Under baseline conditions, surviving juveniles declined from about 1.75 million entering the Klamath River to 875,000 reaching the ocean and about 250,000 surviving ocean entry to age two. Larger pre-smolts were less sensitive to these losses than fry and small parr (Table 3, Outmig. T1; Appendix E, Figures 51 through 52; Satterthwaite et al. 2014; Sturrock et al. 2026). Klamath River flow, temperature, and disease scenarios produced large differences in escapement. High-flow, cool, and restoration-optimized scenarios approached but did not reach targets, while warm or stressed scenarios sharply reduced escapement (Table 3, Outmig. T2; Appendix E, Figures 53 through 54). These results identify downstream survival as a strong candidate constraint.

Estuary monitoring also supports treating the estuary and nearshore period as a growth-and-survival stage rather than only a migration corridor, although current data do not reliably separate Trinity-origin from Klamath-origin fish (Wallace and Collins 1997; Foote et al. 2002; Chen et al. 2023; Schuiteman et al. 2024). Outmig. T3 could not be completed with the final model structure because increasing Trinity River production also changed juvenile abundance, size, and emigration timing. The model therefore could not hold the original outmigration structure constant while isolating whether additional production offset downstream mortality. This hypothesis remains unresolved rather than unsupported.

Table 1 identifies the three outmigration hypotheses, Table 2 lists the three planned tests, and Table 3 distinguishes the two completed tests from Outmig. T3, which could not be completed with the final model structure. Table 4 summarizes the resulting life-stage classification and data needs. Appendix E, Figures 51 through 54, presents the completed results.

11.7 Ocean maturation and survival

This section evaluates hypotheses H_{14} through H_{15} related to ocean survival and harvest (Table 1). Ocean survival and harvest strongly affect whether freshwater production becomes adult escapement (Crozier et al. 2021; Kendall et al. 2023). Poor marine survival or high harvest can mask benefits from freshwater restoration, especially when juveniles enter the ocean small, early, or in poor condition (Gamble et al. 2018; Zabel and Williams 2002; Weitkamp et al. 2015). Ocean harvest produced one of the largest model responses: a 25% reduction more than tripled escapement, and a 50% reduction resulted in exceeding the recovery target; adding in-river harvest reductions increased the response, but ocean harvest remained dominant (Table 3 Ocean T1; Appendix E. Expanded LFA results, Figures 55 through 56). These scenarios support interpreting ocean harvest as a primary limiting factor, although it is outside TRRP control and recovery targets include sustaining fisheries. Favorable first-year ocean conditions increased escapement by about twenty thousand adults relative to unfavorable conditions. The model is parameterized to represent the observed stock-specific relationship between the Pacific Decadal Oscillation and Klamath–Trinity Chinook salmon performance, which differs from the general expectation that positive PDO conditions are often unfavorable for many West Coast salmon populations; this relationship should therefore be treated as stock-specific rather than a general ocean-climate rule (Table 3 Ocean T2; Appendix E. Expanded LFA results, Figures 57–58; Mantua 2015; Quiñones et al. 2014). A final survival-cascade diagnostic indicated that most modeled attrition occurs between Trinity emigration and ocean entry, with larger fish surviving better when size structure is preserved (Table 3 Ocean T3; Appendix E. Expanded LFA results, Figures 59 through 60). Together, these results support the interpretation that ocean and early marine survival are primary systemwide constraints, while reinforcing that Trinity River actions still matter because they shape the fish entering that pathway. Because harvest strongly affects whether restoration gains return as adults, TRRP should use this result to inform coordination with fishery resource agencies, consistent with the decision process outlined here. Harvest mortality and non-harvest ocean survival are evaluated as separate processes: harvest removes fish through age-specific fisheries, whereas ocean survival represents mortality associated with ocean entry, productivity, predation, disease, and other marine conditions. Their scenario effects should not be combined or interpreted as evidence for the same mechanism. Table 1 identifies the ocean hypotheses, Table 2 shows four ocean tests, Table 3 summarizes Ocean T1 through T4 and their Appendix E figure links, and Table 4 carries the ocean interpretation into the life-stage classification matrix. Appendix E, Figures 55 through 61, provides the supporting ocean harvest, early marine survival, survival-cascade, and nested limiting-factor scenario results.

11.8 Synthesis across stages

The analysis supports the historical focus on restoring juvenile rearing habitat: juvenile rearing capacity and growth opportunity remain the strongest direct TRRP management levers because they shape the abundance, size, timing, condition, and life-history diversity of fish entering the downstream survival pathway. The findings also show why habitat restoration alone has not produced the full expected adult response. Under the scenarios tested, harvest and survival through the Klamath River, estuary, early marine period, and ocean exerted the strongest systemwide constraints. The appropriate future strategy is therefore to continue protecting and improving the freshwater foundation while expanding monitoring, scenario testing, and partner coordination beyond the Trinity River. Spawning-to-emergence factors remain compounding or episodic priorities, particularly where local conditions or disturbances could reduce performance.

The management significance of these results is that the large, modeled effects of ocean survival and harvest do not diminish the value of Trinity River restoration. Trinity conditions shape the quantity and quality of juveniles entering the downstream survival pathway. Improving rearing habitat, food, temperature, and migration opportunity can produce more juveniles in better condition while sustaining variation in size, timing, and life history. Because different migrant types succeed under different conditions, preserving this diversity spreads risk and increases the likelihood that part of each cohort will survive variable downstream and ocean conditions, consistent with the salmon portfolio effect (Schindler et al. 2010; Griffiths et al. 2014).

The LFA process also identified an opportunity to strengthen how monitoring information is collected, managed and used across the program. TRRP should establish a program-wide data stewardship framework that links each monitoring activity to a clear management question or hypothesis and applies consistent procedures for data collection, quality control, documentation, version tracking, storage, and release (Wilkinson et al. 2016; Jones et al. 2019; Bledsoe et al. 2022). Study plans and changes in methods should be documented and communicated across participating organizations so that results remain comparable through time (Jones et al. 2019; Bledsoe et al. 2022). A single quality-controlled dataset, supported by clear descriptions of the data and an archived revision history, would reduce duplicated effort, support repeatable analyses, and make existing monitoring investments more useful for adaptive management (Wilkinson et al. 2016; Bledsoe et al. 2022).

Consistent with Merz et al. (2013), monitoring should focus on the life-stage transitions and environmental relationships needed to test restoration hypotheses, rather than collect information without a clear, defined analytical purpose. Where practical, TRRP should build on proven regional approaches rather than develop separate systems. The Healthy Rivers and Landscapes science framework provides a useful example of coordinating hypotheses, common measures, compatible datasets, monitoring, analysis, and decision support across programs (CNRA 2024).

The results should also be read as carryover effects, not isolated stage responses. Gravel suitability is not only a reach-scale habitat attribute; it interacts with adult body size, sex ratio, age structure, and redd-construction behavior. The decoupling framework described by Merz et al. (2024) is relevant here because restoration or augmentation can increase the availability of coarse substrate, but that substrate may not translate into proportional reproductive benefit if the spawning population is increasingly composed of smaller females. Harvest, hatchery influence, or other selective processes that reduce the proportion of older and larger adults could therefore compound gravel-related constraints by reducing the ability of females to construct redds in coarser material, lowering effective spawning capacity or increasing the sensitivity of egg-to-fry survival to substrate conditions (Riebe et al. 2014; Merz et al. 2024). We assume hatchery-origin fish that return younger or smaller and spawn naturally may face the same or greater constraint (Williamson et al. 2010; Christie et al. 2014).

Fine sediment should also be interpreted as a conditional and potentially confounding factor. Under current or moderate sediment conditions, model results suggest fine sediment is not a primary limiting factor. However, that interpretation could change if wildfire, landslides, road failures, or other watershed disturbances increase fine-sediment delivery to spawning reaches. In those years or reaches, fine sediment could reduce intragravel flow, dissolved oxygen delivery, egg-to-fry survival, and fry emergence while also obscuring the expected benefits of gravel augmentation or flow management. For this reason, fine sediment should remain in the diagnostic framework as an episodic risk and as a monitoring priority following major sediment-producing events. The LFA supports testing potential stressors and management actions for both spawning and incubation scenarios.

Juvenile life histories work the same way: producing more fry-sized migrants can increase the number leaving the Trinity River, but those smaller fish may have lower estuary and early ocean survival, particularly under stressful or extreme environmental conditions (Weitkamp et al. 2015; Gamble et al. 2018; Sturrock et al. 2026). In contrast, later-emigrating fish are often larger and may have higher individual survival, but they also face an increased risk of missing downstream migration windows, particularly in the lower Klamath River where water quality decreases and flows decline through the season (Perry et al. 2018a, 2018b; Plumb et al. 2025). This creates a fundamental trade-off between size-dependent survival benefits and timing-dependent migration risks.

The life-cycle model provides a useful framework for exploring this trade-off as a scenario-testing exercise, allowing different size–timing strategies to be evaluated under varying water-year types and future climate scenarios. This type of analysis could help identify conditions under which earlier or later emigration strategies are more favorable and improve the ability to align Trinity River flow and habitat management with downstream survival constraints (Apgar et al. 2021; Kendall et al. 2023).

12. Phase 2 Synthesis and Prioritization

TRRP implementation measures, such as completed rehabilitation sites, restored acreage, sediment placement, and managed flow releases, remain important for documenting delivery and accountability. A complementary set of biological effectiveness measures is needed to determine whether those actions function as intended for salmon. These measures should include spawning and rearing capacity, survival from egg to fry, juvenile growth and condition, migration timing, smolt survival, and adult returns, with each measure tied to a stated LFA hypothesis and decision threshold (Plumb et al. 2023; Stantec Consulting Services 2023; TRRP 2024).

A practical adaptive management sequence is: management action, change in habitat quantity or quality, change in capacity, growth, or survival, successful transition to the next life stage, and contribution to adult production. Applying this sequence to the highest priority hypotheses would make better use of existing TRRP datasets, identify remaining bottlenecks, and focus new sampling on information capable of changing management decisions rather than on additional descriptive metrics alone.

Table 5 translates the life-stage diagnosis into action, monitoring, scenario-testing, and coordination priorities based on expected biological impact, evidence strength, and TRRP's ability to influence each factor. Figure 5 summarizes the decision logic.

The analysis supports three management conclusions. First, TRRP should continue improving juvenile rearing survival, habitat capacity, growth opportunity, and temperature because these are the strongest factors the program can directly influence. Second, TRRP should broaden performance evaluation beyond habitat area and juvenile abundance to include juvenile size, timing, condition, life-history diversity, and survival after leaving the Trinity River. Third, because ocean harvest, age-specific ocean survival, and Klamath River disease and temperature produced the largest modeled effects on adult escapement, TRRP should treat coordination with fishery, Klamath Basin, estuary, and ocean partners as a core recovery strategy rather than a secondary monitoring activity. In the nested scenario, ocean factors produced the largest initial increase, Klamath River conditions produced the next increase, and Trinity River rearing conditions produced the final increase.

For interpretation, the LFA separates five categories that are often conflated. Primary limiting factors are large enough, under the scenarios tested, to explain much of the adult escapement gap. Compounding factors affect production, survival, or carryover traits but do not close or explain the adult-return gap on their own. Episodic factors matter mainly during disturbance years, extreme conditions, or narrow life-stage windows. Data-priority factors are those where uncertainty limits confidence in the diagnosis. Management-priority factors are those where action, monitoring, or coordination is most likely to improve outcomes or reduce decision-relevant uncertainty.

Within that interacting life cycle, juvenile rearing capacity and growth remain the strongest direct TRRP habitat levers because they determine the size, timing, condition, and diversity of juveniles entering downstream and marine environments. Model results indicate that Trinity River production can meet or exceed recovery targets when post-emigration survival is favorable. For TRRP, the most actionable conclusion is that rearing improvements should be evaluated by whether they increase the number of juveniles that leave the Trinity River at sizes, times, and conditions likely to survive downstream, not by habitat area or juvenile abundance alone.

The management implication is that Trinity restoration, downstream survival, ocean conditions, and harvest must be addressed as connected parts of the same recovery strategy. Because harvest and ocean survival had the largest modeled effects, TRRP should use the LFA to engage fishery and resource agencies in evaluating how harvest and marine conditions affect the return on freshwater restoration investments, identify scenarios that could materially change adult escapement, and align monitoring across the Trinity River, Klamath River, estuary, and ocean. Within the Trinity River, the program should continue emphasizing rearing habitat, food web support, temperature management, floodplain connectivity, and spawning substrate management while tracking whether those actions improve juvenile size, timing, condition, diversity, and subsequent survival.

The main uncertainties that affect this synthesis are those that govern how effects carry forward across stages: empirical rearing capacity, size- and timing-dependent survival during downstream migration, Trinity River-origin survival through the Klamath River, estuary, and early marine period, reach-scale spawning and incubation habitat, egg-to-fry survival, adult holding behavior, and naturally produced yearling life histories. These uncertainties are carried forward into the prioritization framework by distinguishing factors that are high impact, directly manageable, weakly supported, or primarily external to TRRP control.

The prioritization process follows a simple decision tree (Figure 5). First, each candidate factor is screened for expected biological impact on adult escapement or key carryover traits such as juvenile size, timing, condition, and life-history diversity. Factors with low or episodic effects remain in the framework but receive lower immediate priority unless conditions change. Factors with unclear or high expected impact are then screened by evidence strength. If support is weak, the factor becomes a data priority because better information could change the diagnosis. If support is strong, the next question is TRRP's role. Factors within direct TRRP control become priority actions. Factors that TRRP can partly influence require both local action and partner coordination. Factors mostly outside TRRP control become coordination priorities, supported by scenario planning and regional monitoring. The decision tree should be read as an alternative-strategy framework: factors with strong evidence and direct TRRP control point to action; factors with high uncertainty point to monitoring or model refinement; factors outside TRRP control point to coordination and scenario planning. Scenario testing supports this alternative-strategy framework by showing how ocean, Klamath River, and Trinity River conditions interact. The LFA identifies which action-specific scenarios should be prioritized for future model testing and adaptive management decisions.

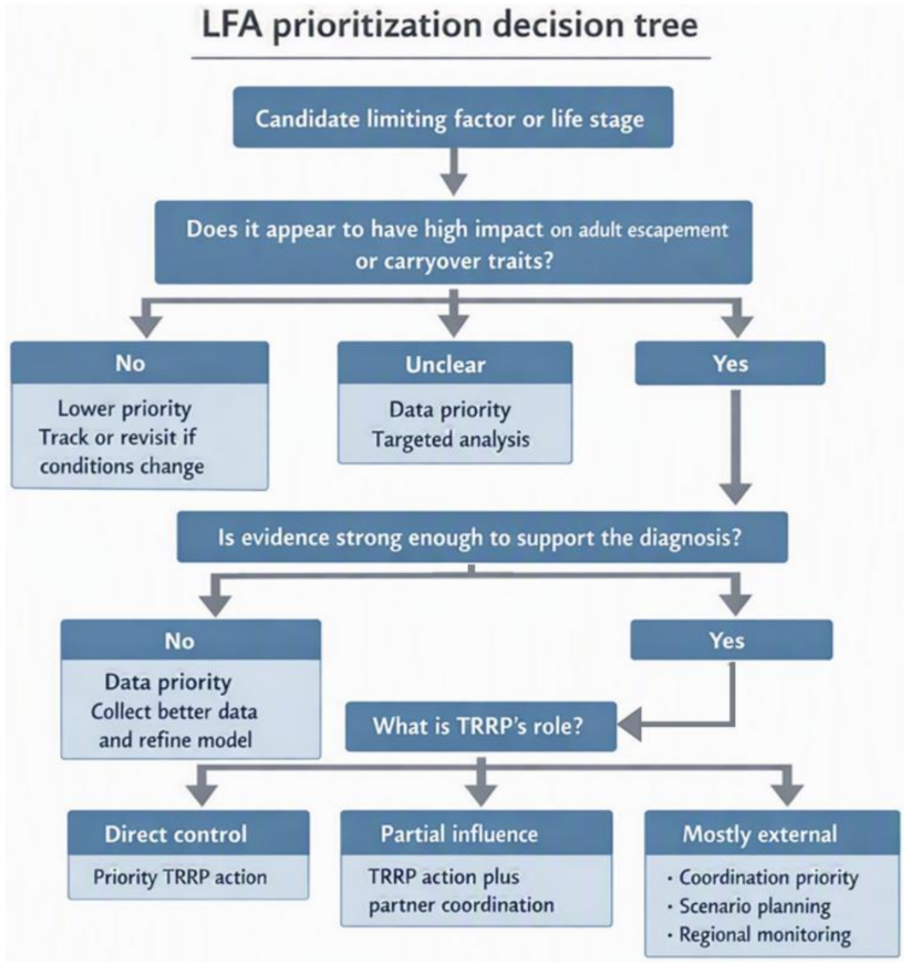

Figure 5. Decision tree used to translate Limiting Factors Analysis (LFA) results into action, data, monitoring, or coordination priorities based on expected impact, strength of evidence, and Trinity River Restoration Program (TRRP) role.

Table 4 summarizes the diagnostic findings by life stage, including classifications and priority data needs. Table 5 builds on that synthesis by identifying management priorities, potential TRRP actions, and key caveats. Primary systemwide factors include downstream migration, estuary and early marine survival, ocean conditions, and harvest. The strongest direct TRRP priority is improving and calibrating juvenile rearing capacity and growth opportunity. Spawning and incubation factors are generally compounding but remain important where they affect carryover traits or episodic risks. Data priorities include rearing capacity, size- and timing-dependent downstream survival, Trinity River-origin estuary and early marine survival, reach-scale spawning and incubation habitat, egg-to-fry survival, adult holding behavior, and naturally produced yearling life histories.

Table 4. Life-stage classification matrix of limiting factors and life stages, with supporting evidence from limiting factors analysis (LFA) Tests (see Table 3), TRRP's role or ability to influence a life stage or limiting factors in that life stage, level of confidence (Conf.) related to data gaps and uncertainties in parametrizing the LCM, and key data needed to address the uncertainties.

Life Stage	Classification	LFA Test Evidence	TRRP Role	Conf.	Key Data Need
Adult immigration and holding	Compounding; episodic	T1–T4; Figures 1-15 Appendix E	Partial; Klamath external	Med.	Holding-habitat use and behavior
Spawning	Compounding; lower priority	T1–T4; Figures 1-15 Appendix E	Direct	Med.	Reach-scale spawning capacity and substrate data
Incubation and emergence	Compounding; not primary	T1–T6; Figures 16-29	Direct to partial	Med.	Spawning-gravel suitability, fine sediment, and egg-to-fry survival
Juvenile rearing	Strongest in-river candidate; high leverage	T1–T6; Figures 30-50	Direct	Med.–High	Empirical rearing capacity and yearling life-history data
Outmigration / estuary / early marine	High-priority downstream constraint	T1, T2; Figures 51-54	Partial	Med.	Traps below confluence; run type origin at traps; estuary origin-ID and survival
Ocean maturation and harvest	Primary systemwide	Ocean T1–T2; Figures 55-61	Mostly external	High / Med.–High	Trinity-specific tag data, ocean indices, and stock-split reconstruction

The central conclusion is that the model did not identify one isolated Trinity River bottleneck. Instead, it shows how Trinity River restoration, downstream survival, ocean conditions, and harvest interact to determine adult returns. This clarifies where TRRP has direct leverage and where coordination is needed so freshwater gains can return as adults.

12.1 Summary of key takeaways for a general audience

The LFA identifies juvenile rearing habitat, growth opportunity, size, timing, condition, and life-history diversity as TRRP's strongest direct restoration levers. Adult returns also depend on survival through the Klamath River, estuary, ocean, and harvest pathway. TRRP should therefore pair freshwater restoration and monitoring with scenario testing and coordination with downstream and fishery partners.

In plain terms, this analysis does not say Trinity River restoration is ineffective. It gives the program a clearer opportunity to focus restoration on the juvenile traits most likely to carry forward, fill the data gaps that would change decisions, and coordinate early with basin, estuary, ocean, and fishery partners so restoration gains have the best chance to become stronger adult returns.

Table 5 presents alternative strategy pathways by linking each diagnostic result to the appropriate response: action, monitoring, scenario testing, coordination, or lower-priority tracking.

Table 5. Alternative chronological diagnostic summary linking diagnostic results to TRRP response categories. Impact reflects the estimated effect on adult escapement or key carryover traits, Support reflects the strength of evidence, and Priority / TRRP Action identifies the recommended management response. Impact, Support, and Priority / TRRP Action categories are defined below the table so readers can distinguish biological effect size, confidence in the evidence, and the recommended management response.

Order	Life Stage	Test	Adult Escapement Interpretation	Impact	Support	Priority / TRRP Action	Basis / Caveat
1	Adult immigration	Adult Imm. T1	Improved immigration survival increased escapement but did not reach the target alone.	Moderate	Moderate	Targeted monitoring	Model result; assumptions about Klamath–Trinity survival.
2	Adult holding	Adult Imm. T2	Holding capacity had little effect under baseline harvest.	Low	Low	Defer / low priority	Applies mainly to spring-run; limited data.
3	Spawning	Adult Imm. T3 / Spawning T3	Spawning capacity reduced escapement mainly under large reductions.	Moderate	Moderate	Targeted monitoring	Coarse test; fine-scale competition uncertain.
4	Adult immigration / habitat	Adult Imm. T4 / Spawning T4	Remaining limitation shifted toward Trinity habitat, especially rearing.	Moderate	Moderate	Actionable management target	Consistent signal; capacity estimates important.
5	Incubation / emergence	Incub. T1	Improved incubation increased escapement but did not meet the target.	Moderate	Moderate	Targeted monitoring	Stage remains data-poor.
6	Redd construction	Incub. T2	Coarse gravel reduced escapement by limiting redd construction.	Moderate	Low–Moderate	High data priority	Strong mechanism; limited spatial data.
7	Incubation / emergence	Incub. T3	High fine sediment	Moderate	Low–Moderate	High data priority	Limited spatial fines data.

Order	Life Stage	Test	Adult Escapement Interpretation	Impact	Support	Priority / TRRP Action	Basis / Caveat
			reduced survival.				
8	Incubation	Incub. T4	Disturbance mattered mainly under extreme conditions.	Conditional	Low–Moderate	Defer / episodic	Episodic effect.
9	Incubation	Incub. T5	Thiamine deficiency mattered under severe conditions only.	Conditional	Low	Defer / episodic	Assumption-dependent.
10	Incubation / emergence	Incub. T6	Improved incubation increased escapement but not to target.	Moderate	Moderate	Targeted monitoring	Not sufficient alone.
11	Juvenile rearing	Rearing T1	Rearing capacity strongly affected size, timing, and escapement.	High	Low-Moderate	Top management priority	Strong signal; Trinity rearing capacity data limited.
12	Juvenile rearing	Rearing T2	Food increased escapement only when sustained.	Conditional	Moderate	Targeted monitoring	Compounding effect.
13	Juvenile rearing	Rearing T3	Temperature affected growth and survival tradeoffs.	Moderate	Moderate	Actionable management target	Strong mechanism; manageable via flow.
14	Rearing / downstream	Rearing T4	Trinity production met targets when downstream survival improved.	High	Moderate–Strong	High data priority	Indicates downstream limitation.
15	Juvenile rearing	Rearing T5	Hatchery timing altered size distribution, little effect on escapement.	Low	Low	Defer / low priority	Placeholder assumptions.

Order	Life Stage	Test	Adult Escapement Interpretation	Impact	Support	Priority / TRRP Action	Basis / Caveat
16	Juvenile rearing	Rearing T6	Rearing changes affected adult returns mainly through emigrant size and timing, not abundance alone; larger, better-timed emigrants had higher downstream survival.	High	Low–Moderate	High data priority / management-relevant test	Size and timing response is modeled and biologically plausible, but support remains limited by uncertainty in flow–habitat relationships, habitat quality, and size-dependent downstream survival.
17	Outmigration	Outmig. T1	Large losses occurred through Klamath and estuary.	High	Moderate	Actionable / coordination priority	Baseline-only but strong signal.
18	Outmigration	Outmig. T2	Flow, temperature, and disease produced large differences.	Moderate–High	Moderate	Actionable / coordination priority	Important episodic constraint.
19	Ocean / harvest	Ocean T1	Reducing harvest produced large escapement increases.	High	Moderate–Strong	Policy / coordination priority	Outside TRRP control.
20	Ocean / early marine	Ocean T2	Early marine conditions produced strongest survival signal.	High	Strong	Policy / coordination priority	High-probability constraint.
21	Ocean entry	Ocean T3	Major attrition before ocean entry, size-dependent survival.	High	Moderate	Actionable / coordination priority	Supports downstream limitation.
22	Whole life cycle	Ocean T4	Coordinated ocean, Klamath, and Trinity improvements increased modeled escapement	High	Moderate	Integrated priority: TRRP rearing actions + basin/ocean coordination	Synthesis scenario; high modeled impact depends on combined external and Trinity actions, so it supports

Order	Life Stage	Test	Adult Escapement Interpretation	Impact	Support	Priority / TRRP Action	Basis / Caveat
			from baseline to 68,035 adults.				both direct rearing priorities and basin/ocean coordination rather than a single management action.

Definitions for Table 5 classifications:

Impact describes modeled or inferred biological effect on adult escapement or key carryover traits.

- **High** = large effect that can strongly change adult escapement or substantially alter size, timing, condition, or life-history diversity;
- **Moderate-high** = strong effect that is not clearly dominant but could materially influence prioritization;
- **Moderate** = meaningful effect that can influence interpretation or management but does not explain the adult-return gap alone;
- **Conditional** = effect depends on thresholds, disturbance years, specific reaches, life stages, or scenario assumptions;
- **Low** = small, bounded, or weak effect under the scenarios tested.

Support describes confidence in the classification.

- **High** = supported by strong model response, relevant empirical data, or multiple consistent lines of evidence;
- **Moderate-high** = generally well supported but with remaining uncertainty that could affect magnitude or implementation; **Moderate** = supported by model results or evidence but dependent on assumptions, surrogate data, or incomplete local information;
- **Low-moderate** = plausible but weakly supported, indirect, or sensitive to assumptions; **Low** = limited evidence or high uncertainty.

Priority / TRRP Action defines the management response:

- **Direct action** = substantially within TRRP authority, program footprint, or restoration toolbox;
- **Action + monitoring** = act or refine an action while measuring whether the expected biological response occurs;
- **Targeted monitoring** = collect specific, repeatable data to resolve decision-relevant uncertainty before changing or prioritizing management;
- **Scenario testing** = use the life cycle model or graphical user interface to compare plausible future conditions or management alternatives;
- **Coordination** = work with Klamath Basin, estuary, ocean, harvest, hatchery, regulatory, or other partners because the factor is only partly within TRRP influence;
- **Defer / low priority** = retain the factor in the diagnostic framework but do not emphasize immediate action because the modeled effect was small, bounded, or unlikely to change near-term decisions;
- **Defer / episodic** = retain the factor as a conditional risk that may require attention during disturbance years, extreme environmental conditions, specific reaches, or narrow life-stage windows.

13. Data Gaps and Key Uncertainties

Monitoring priorities are limited to uncertainties that could change a management decision or the ranking of limiting factors (Table 6). Essential needs are empirical Trinity River rearing capacity and its effects on juvenile size and timing; Trinity-origin survival through the Klamath River, estuary, and early marine period; and post–Klamath dam-removal changes in downstream survival (Table 6). Managers should not wait for these data to act: TRRP should continue improving juvenile rearing habitat, growth opportunity, temperature, and life-history diversity; evaluate actions with size, timing, condition, and subsequent survival rather than abundance alone; use the LCM to test proposed flow and habitat strategies before implementation; and coordinate with downstream, ocean, hatchery, and fishery partners. Other gaps, including finer-scale spawning habitat, egg-to-fry survival, adult holding, predation, and yearling life histories, are desirable refinements unless new evidence shows they could alter a near-term decision.

This section focuses on uncertainty rather than restating the limiting-factor diagnosis. Several classifications depend on generalized assumptions because direct Trinity River-specific data are limited. Those assumptions are reasonable for a Phase 2 analysis, but they should be treated as hypotheses to test, not final answers (Colson and Cooke 2018; Hemming et al. 2018; Roni et al. 2018; Camac et al. 2021).

Priority uncertainties are those that affect interactions among stages, not simply isolated parameter values. These include juvenile rearing capacity; survival and size-selective mortality during Trinity–Klamath outmigration; Trinity River-origin survival through the estuary and early ocean; naturally produced yearlings; egg-to-fry survival; reach-scale spawning-gravel suitability and fine sediment; adult holding behavior; hatchery-release schedules; run-type identification beyond adult migration; and stock-split limitations in Klamath–Trinity tag or cohort data. These data gaps matter because they influence how freshwater habitat actions translate into downstream survival and adult returns.

These uncertainties affect hypotheses related to juvenile rearing (H_9 through H_{11}), downstream migration and survival (H_{12} through H_{13}, H_{18} through H_{19}), incubation (H_5 through H_8), and adult immigration, holding, and spawning (H_1 through H_4). The key question is whether better data would change the diagnosis or the management priority. Factors with high expected effect and weak support should be addressed first.

Monitoring should focus first on uncertainties that could change management interpretation: rearing capacity and growth, size- and timing-dependent downstream survival, Trinity River-origin survival through the estuary and early marine period, and reach-scale spawning-to-emergence conditions. Lower-impact or episodic factors should stay in the framework, but they do not warrant the same monitoring effort unless new evidence or disturbance events increase their expected effect.

The 2024 removal of four hydroelectric dams on the Klamath River adds an important source of uncertainty. Dam removal has reconnected historical habitat and is altering flow, temperature, sediment transport, water quality, and fish passage conditions (NOAA Fisheries 2024; California State Water Resources Control Board 2024). These changes may affect adult immigration and juvenile outmigration through the lower Klamath River and estuary, but the direction and magnitude of survival effects remain uncertain during the early post-removal transition, including potential changes in myxozoan disease dynamics (Bartholomew et al. 2023;

Bartholomew et al. 2026). Rather than creating a separate set of priorities, dam removal reinforces the need for basin-wide monitoring and for model scenarios that test alternative assumptions about adult and juvenile survival in the Klamath River.

Table 6. Prioritization of data gaps and uncertainties to inform future monitoring and refinement of the life cycle model and limiting factors analysis. See Table 1 for hypotheses.

Priority Tier	Life Stage	Key Data Gap / Uncertainty	Affected Hypotheses (Table 1)	Why it Matters for LFA Diagnosis	Recommended Action
Tier 1	Juvenile rearing	Empirical rearing capacity, density dependence, growth, survival	H_9–H_{11}	Strongest Trinity-managed lever; current estimates drive model sensitivity but are weakly constrained	Direct field studies + capacity calibration
Tier 1	Outmigration (Trinity–Klamath)	Survival rates, size-selective mortality, migration timing; lack of traps below confluence	H_{12}–H_{13}, H_{18}–H_{19}	Major uncertainty in where mortality occurs and how size/timing affects survival	Install/expand monitoring (RSTs, tagging)
Tier 1	Estuary & early marine	Trinity-origin identification, survival, growth, residence time	H_{12}–H_{13}, H_{15}	Prevents separation of Trinity vs Klamath mortality; limits core systemwide diagnosis	Stock ID methods + estuary survival studies
Tier 2	Juvenile life history	Proportion and survival of naturally produced yearlings (1+ fish)	H_9, H_{11}, H_{17}	Limits understanding of life-history diversity and carryover effects	Targeted yearling monitoring + tagging
Tier 2	Incubation & emergence	Spatial distribution of coarse substrate, fine sediment, egg-to-fry survival	H_5–H_8	Drives spawning-to-emergence survival but currently based on coarse assumptions	Reach-scale habitat mapping + survival studies
Tier 2	Cross-stage processes	Carryover effects linking size, timing, and condition across stages	H_{16}–H_{17}	Limits integration of life-cycle dynamics and tradeoffs central to the LFA	Integrated tagging + life-cycle studies
Tier 3	Ocean & harvest	Trinity-specific tag data, stock composition, harvest attribution	H_{14}–H_{15}	Reduces precision in identifying ocean vs harvest effects	Improved stock-specific tagging and modeling
Tier 3	Outmigration conditions	Flow–temperature–disease interactions in Klamath corridor	H_{12}, H_{15}	High variability and episodic mortality not fully resolved	Coordinated basin monitoring + modeling
Tier 4	Spawning	Reach-scale spawning capacity, redd superimposition, habitat distribution	H_4	Affects density dependence but only becomes limiting under extreme scenarios	Habitat surveys + finer-scale modeling

Priority Tier	Life Stage	Key Data Gap / Uncertainty	Affected Hypotheses (Table 1)	Why it Matters for LFA Diagnosis	Recommended Action
Tier 4	Adult holding	Holding habitat use, density, behavior, temperature thresholds	H_2–H_3	Currently non-limiting but uncertain under higher escapement scenarios	Targeted behavioral studies
Tier 4	Hatchery interactions	Release timing, contribution, natural-origin interactions	H_{11}	Limited effect in current tests; secondary influence on size structure	Refine assumptions if management actions change
Tier 5	Adult Immigration	Routing and survival	H_2	Appears compounding or context-dependent rather than primary.	Continue monitoring and refine survival estimates as post-dam-removal conditions develop.
Tier 5	Episodic stressors	Hydrologic disturbance, thiamine deficiency prevalence	H_8	Episodic, condition-dependent effects; not primary drivers under typical conditions	Periodic assessment, not intensive monitoring

14. Applications and Next Steps

This section translates the diagnosis into program use. The LFA should guide restoration design, monitoring, and coordination by keeping the full life cycle in view. Trinity actions should be evaluated by how they affect juvenile traits entering downstream survival pathways, while basin-scale monitoring and scenarios should be used to understand how those benefits carry through different Klamath and ocean conditions (Booth et al. 2016; Jorgensen et al. 2021; Kendall et al. 2023).

14.1 Applications for TRRP Management

The results point to three uses for TRRP: direct actions within the Trinity River, coordination with partners on downstream and marine processes, and focused data collection where uncertainty affects decisions.

Direct Trinity River actions: Within TRRP's primary scope of influence, the results support actions that improve juvenile rearing capacity, growth opportunity, and life-history diversity. Flow management, channel rehabilitation, floodplain restoration, food-web support, temperature management, and spawning-substrate management should be evaluated by how they affect the size, timing, condition, and diversity of juveniles emigrating from the Trinity River. Because those traits influence downstream and marine survival, rearing and spawning actions should be designed and monitored as part of a connected life-cycle pathway rather than as stand-alone habitat improvements. Recommended near-term actions include targeted field surveys of juvenile rearing habitat, bathymetric and topographic surveys to quantify channel and floodplain habitat availability, and flow-habitat modeling, including two-dimensional habitat modeling where appropriate, to estimate how the quantity and quality of usable rearing habitat change across flows, seasons, and restoration treatments.

Coordination beyond the Trinity River: Downstream migration through the Klamath River, estuary, and early marine period, along with ocean conditions and harvest, strongly influence whether freshwater production becomes adult escapement. Although many of these processes are outside direct TRRP control, TRRP can improve the diagnosis by contributing to regional monitoring, supporting studies that link Trinity-origin fish to downstream survival, and participating in interagency processes related to Klamath River conditions, harvest management, and ocean research.

Monitoring and adaptive management: Monitoring should focus where new data would change the diagnosis or management priority. Highest priorities include empirical rearing capacity, growth and density dependence, size- and timing-dependent survival during outmigration, Trinity River-origin survival through the Klamath River, estuary, and early marine period, reach-scale spawning and incubation habitat, and naturally produced yearling life histories. For juvenile rearing, the priority is to pair biological monitoring with habitat quantification: field surveys should document fish use, density, size, timing, and growth across habitat types; bathymetric and topographic surveys should define available channel-margin, side-channel, alcove, and floodplain habitats; and flow-habitat modeling, including two-dimensional hydraulic and habitat models, should estimate how habitat quantity, depth, velocity, cover, temperature exposure, and connectivity vary under alternative flow and restoration scenarios.

14.2 Integrated Programmatic Next Steps

The Phase 2 Trinity River Chinook salmon LFA provides a current life-cycle diagnosis and decision-support framework for TRRP adaptive management. As priority data gaps are reduced, the model can be updated and the limiting-factor interpretation refined to reflect new empirical evidence, changed environmental conditions, and additional scenario testing.

Because the life-cycle model was built with open-source code and a graphical user interface, assumptions can be reviewed and updated as new information becomes available. This should make future revisions easier and help reviewers see how changes in inputs affect the diagnosis.

Future model applications should evaluate management scenarios involving flow, habitat, harvest, climatic conditions, and downstream survival. Scenario design should explicitly represent the greater climatic and hydrologic variability projected for California, including stronger atmospheric-river storms, larger floods alternating with drought, declining snowpack, a greater proportion of precipitation falling as rain, and more intense runoff events (Gershunov et al. 2025). Testing these conditions across multiple water-year sequences would help determine whether current limiting-factor classifications remain stable and which combinations of flow, habitat, and downstream survival actions are most robust under a wider range of future conditions. The current LFA includes a subset of possible diagnostic tests; additional tests can be developed as TRRP identifies new questions, improves data inputs, or evaluates emerging management needs.

14.3 Overall Management Implication

The main management implication is that TRRP should pursue an integrated strategy: improve juvenile production, growth, and life-history diversity within the Trinity River; monitor whether those improvements persist through downstream and marine survival; and coordinate with external agencies where key constraints extend beyond TRRP authority. This framing avoids treating any single life stage as independent and keeps management focused on the full pathway from restoration action to adult escapement.

15. Conclusions

The current LFA builds on, rather than replaces, the historical Trinity restoration paradigm. The 1988 restoration framework and the Trinity River Flow Evaluation Study identified altered flow, sediment supply, channel form, and juvenile rearing habitat as central consequences of Trinity River Division operations and established flow, sediment, and channel rehabilitation as primary restoration tools (U.S. Fish and Wildlife Service 1988; U.S. Fish and Wildlife Service and Hoopa Valley Tribe 1999). The present analysis supports continued emphasis on juvenile rearing as TRRP's strongest direct habitat lever, while adding that achievement of adult escapement objectives also depends strongly on survival through the Klamath River, estuary, early marine period, ocean, and fisheries.

Historical escapement should not be treated as evidence of a single historical habitat condition. Adult returns reflect survival across the full life cycle, whereas sediment supply and channel form changed through mining, logging, dam construction, flow regulation and diversion, sediment trapping, and subsequent restoration. Historical escapement and sediment conditions therefore provide context for restoration objectives but do not isolate the life stage or process responsible for present limitations.

The LFA met its diagnostic objectives by identifying the life stages, transitions, and factors that most constrain modeled adult escapement and by distinguishing constraints TRRP can manage directly, influence through coordination, or account for in planning. Under the modeled scenarios and current assumptions, the largest constraints occur after juveniles leave the Trinity River, particularly during passage through the Klamath River, estuary, early marine period, and ocean, and through harvest. These factors largely determine whether freshwater production returns as adults. Because they occur partly or wholly outside the Trinity River, TRRP cannot manage them directly; their implications must be addressed through coordinated monitoring, scenario planning, and engagement with Klamath Basin, estuary, ocean, hatchery, and fishery partners.

Within the Trinity River, the strongest direct TRRP lever is juvenile rearing. Flow, temperature, channel rehabilitation, floodplain connectivity, sediment management, and related habitat actions can improve rearing capacity, growth opportunity, survival, and the size, timing, condition, and life-history diversity of juvenile outmigrants. Spawning habitat, incubation conditions, adult holding habitat, and episodic stressors remain important, but the LFA classifies them primarily as compounding, conditional, or data-limited under the scenarios tested rather than as the principal systemwide constraints. Their importance may increase in specific reaches, disturbance years, spring-run conditions, or future higher-abundance populations.

The analysis supports continuing TRRP's long-standing investment in juvenile rearing habitat, but it also indicates that the next phase should broaden how success is defined and how recovery is pursued. TRRP should continue hypothesis-driven flow and habitat actions; evaluate whether those actions produce juveniles with the abundance, size, timing, condition, and life history diversity needed to survive downstream; and use the LCM to compare alternative strategies before major new investments. Because harvest and survival after salmon leave the Trinity River can dominate adult outcomes, TRRP should also formalize coordination with Klamath Basin, estuary, ocean, hatchery, and fishery partners. The LFA should be updated as empirical rearing capacity, Trinity origin survival, egg to fry survival, adult holding, yearling life history, and post-Klamath Dam removal data become available. The central conclusion is not that the prior restoration strategy was misplaced, but that its benefits will be best realized through a broader life cycle recovery strategy.

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18. Appendices

These appendices are provided as separate documents to focus the main report on the key findings for a broad audience. The following appendices provide more detailed information and are referenced throughout the report to provide supporting documentation:

- Appendix A. Detailed model structure and transitions
- Appendix B. Assumptions and rules
- Appendix C. Data sources and input requirements
- Appendix D. Calibration and tuning
- Appendix E. Expanded LFA results
- Appendix F. Data gaps and priority uncertainties
- Appendix G. GUI user guide
- Appendix H. Data References