APPENDIX B. ASSUMPTIONS AND RULES

This appendix supports the Limiting Factors Analysis (LFA) for Trinity River Chinook salmon *Oncorhynchus tshawytscha* prepared for the Trinity River Restoration Program and follows the general process outlined in Hamilton and Murphy (2018). It summarizes the assumptions and rules that define the underlying model logic for the life cycle model and LFA testing, including how the LFA tests were structured. Information is organized by life stage.

Each rule follows a consistent evidence hierarchy: (1) Trinity/Klamath-specific data, modeling, and studies were used where available; (2) broader peer-reviewed or technical literature was used when local information was unavailable or incomplete; and (3) where no directly transferable quantitative estimate existed, expert-derived values were used to convert the supported biological mechanism into a model-ready multiplier, threshold, or scenario parameter for calibration and sensitivity testing. Baseline values are favorable reference conditions used to anchor calibration; stressor multipliers are relative reductions from that reference condition.

IMMIGRATION, ESCAPEMENT, AND SPAWNING:

Description of Life Stage Transition:

This life stage transition represents immigration of Chinook salmon from entry into the Klamath River to successful entry into the Trinity River and spawning habitat occupancy. The population of interest consists of spring- and fall-run that, under baseline homing conditions, would be expected to return to the Trinity River.

For these life stage transitions, migration habitat is not capacity-limited but holding habitat (for spring-run only) and spawning habitat for both races are potentially capacity-limited. We consider several rules that determine survival during adult immigration in the Klamath and Trinity rivers, spring-run holding in the Trinity River, and spawning habitat occupancy include:

- Adult immigration survival in the Klamath (thermal stress, disease, and water quality)
- Straying into the Trinity River
- Straying and Trinity River entry (flow split, holding duration, and crowding)
- In-river harvest
- Adult immigration survival in the Trinity (thermal stress, disease, and water quality)
- Holding habitat capacity in Trinity (spring-run only; volume, quality, and temperature)
- Hatchery-origin spawners (spawning habitat competition)
- Spawning habitat area and capacity in Trinity
- Female size and redd construction

These rules determine the abundance of successful spawners and constructed redds, which then determine egg abundance for the next life stage. In-river harvest also affects these stages; although introduced in the LFA testing of ocean harvest rates, it is applied here when estimating river escapement.

Assumptions for LFA and Life Cycle Model (LCM) Rules:

Adult immigration through the Klamath: Elevated water temperature is a dominant driver of immigrant Chinook salmon mortality in the Klamath River, with survival declining sharply as temperatures exceed ~ 20 to 22 °C and exposure duration increases. Laboratory and field studies consistently show that adults experience nonlinear increases in physiological stress, energetic depletion, and pre-spawn mortality under sustained warm conditions, with cumulative thermal exposure (degree-days) often more predictive of mortality than short-term temperature peaks (Strange 2012; Keefer et al. 2018; Isaak and Young 2023). Disease further amplifies temperature-related mortality, particularly in the Klamath River where pathogens such as *Ceratonova shasta*, *Ichthyophthirius multifiliis*, and *Flavobacterium columnare* are strongly temperature- and residence-time dependent; warm, low-flow conditions increase pathogen proliferation, infection intensity, and transmission, converting sublethal thermal stress into lethal outcomes (Bartholomew et al. 2022; Robinson et al. 2022; Strange 2010). Water quality stressors such as low dissolved oxygen also exacerbate these effects by reducing aerobic scope and swimming performance, slowing migration and increasing exposure to both heat and disease (Keefer et al. 2018).

Although Chinook salmon frequently seek cold-water refugia several degrees cooler than the mainstem, prolonged use can delay migration, disrupt homing, and increase straying or failure to reach natal spawning areas (Keefer et al. 2018; Snyder et al. 2022; Isaak et al. 2015). Temperature defines the baseline physiological risk, while disease and low dissolved oxygen compound mortality under warm, low-flow conditions. Temperature categories in Table 1 are based on documented thermal responses, whereas the Table 1 survival multipliers are expert-derived values. Table 2 combines temperature, disease, and water quality into a single survival multiplier rather than applying separate sequential multipliers. The combined values are expert-derived values informed by the documented mechanisms and/or published science and intended for calibration and sensitivity testing. They are not empirical estimates derived from a single study. Users select one Table 2 condition for each run type before model execution, and that condition remains fixed throughout the simulation.

Table 1. Temperature categories used to influence baseline survival during adult migration in the Klamath River.

Temperature	Biological Justification	Survival Multiplier
≤ 18 °C	Temperatures largely within the optimal or near-optimal physiological range for Chinook salmon; low metabolic stress and high aerobic scope. This is the typical default range for spring-run Chinook salmon based on earlier river entry timing (beginning in ~May).	0.98
>18-≤20 °C	Onset of elevated metabolic demand and reduced energetic efficiency; sublethal stress increases vulnerability, but most adults remain migratory. This is the typical default range for fall-run Chinook salmon based on later river entry timing (August to October).	0.95
>20-≤22 °C	Threshold zone where sustained exposure causes rapid energetic depletion, impaired swimming performance, and increased disease susceptibility.	0.85
>22 °C	Temperatures exceed upper tolerance limits for sustained exposure; mortality accelerates sharply due to physiological failure and stress.	0.70

Table 2. Disease exposure categories used to influence survival of immigrating Chinook salmon in the Klamath River and interaction with temperature.

Temperature Bin (≥5–7 Day Exposure)	Disease Condition	Water Quality Condition	Biological Interpretation	Combined Survival Multiplier
≤18 °C	No detectable disease	DO ≥6 mg/L	Near-optimal migration conditions; low metabolic stress and minimal pathogen activity. **Baseline survival under favorable conditions for spring-run Chinook salmon**.	0.98
≤18 °C	Low pathogen presence	DO ≥6 mg/L	Minor disease pressure; limited interaction with temperature. Small disease penalty even under cool conditions.	0.95
18–20 °C	No detectable disease	DO ≥6 mg/L	Onset of elevated metabolic demand; most adults remain migratory. Moderate baseline mortality bin. **Baseline survival under favorable conditions for fall-run Chinook salmon.**	0.95[a], 0.97[b]
18–20 °C	Low–moderate pathogen presence	DO ≥6 mg/L	Sublethal thermal stress combined with early disease amplification. Additive disease penalty in warm-edge conditions.	0.90
20–22 °C	No detectable disease	DO ≥6 mg/L	Threshold zone where sustained exposure drives rapid energetic depletion. High-risk temperature bin even without disease.	0.85
20–22 °C	Moderate pathogen presence	DO ≥6 mg/L	Disease converts thermal stress into significant mortality; infection intensity increases. Primary combined temperature–disease bottleneck.	0.72
20–22 °C	Moderate pathogen presence	DO <6 mg/L	Reduced aerobic scope increases residence time and disease exposure. Justifies water-quality modifier layered on disease penalty.	0.67
>22 °C	No detectable disease	DO ≥6 mg/L	Temperatures exceed sustained tolerance limits; mortality accelerates. Severe thermal stress scenario.	0.70
>22 °C	High pathogen presence / epizootic	DO ≥6 mg/L	Warm-water disease outbreaks cause rapid pre-spawn mortality. Represents documented Klamath epizootic years.	0.55
>22 °C	High pathogen presence	DO <6 mg/L	Compounding stressors (heat, disease, hypoxia) produce catastrophic losses. Upper-bound mortality scenario for Limiting Factors Analysis testing.	0.50

[a] Default value for spring-run Chinook salmon
[b] Tuned and calibrated value for fall-run Chinook salmon

Straying and entry into the Trinity River: Available evidence indicates that Trinity River–origin adult Chinook salmon stray into the Klamath River at low but non-zero rates based on historical coded-wire-tag recoveries (De Jong and Mills 1992; RMPC 2026). Hatchery production can also influence straying when release, acclimation, or imprinting conditions reduce homing fidelity (Westley et al. 2013). Published studies demonstrate that stronger tributary plume signals increase successful homing and tributary selection at major confluences,

while migration delay, prolonged holding, and behavioral disruption can increase straying rates (Keefer et al. 2006; Keefer and Caudill 2014; Strange 2012; Keefer et al. 2018; Westley et al. 2013). The LFA represents Trinity River entry as a threshold-based routing process driven by Trinity River flow share at the confluence, with modifiers for holding duration and crowding. Straying is applied as a survival multiplier because fish that fail to enter the Trinity River are removed from the Trinity spawning population. Users select one Table 3 condition for the full simulation. Because empirical estimates were unavailable, the Table 3 multipliers and the default Klamath-origin straying proportion are expert-derived values.

Because homing errors can occur at major confluences under ambiguous hydraulic, olfactory, or thermal cues, the model also allows a small adjustable contribution of Klamath-origin adults straying into the Trinity River, supported by coded-wire-tag recoveries from the Klamath–Trinity basin (De Jong and Mills 1992; RMPC 2026). This input is an adjustable range from 0 to 1 with a default value of 0.05. This value is proportional to Trinity escapement and added to the total Trinity escapement, proportionally by run and age class. This value is supported by published studies, because there were no known empirical estimates; an expert-derived value was used.

Table 3. Straying and survival rules that influence adult entry into the Trinity River based on flow share, confluence holding duration, and crowding assumptions.

Trinity Flow Share at Confluence	Holding Duration	Crowding / Predation Pressure	Biological Interpretation	Combined Entry Survival Multiplier
≥30% (Strong cues)	No extended holding	Low	Strong hydraulic and olfactory cues dominate routing; most adults enter Trinity. **Baseline straying condition under favorable flow.**	0.95
≥30% (Strong cues)	Extended holding (>10 days)	Low	Holding disrupts migration timing, but strong cues still guide most fish correctly. Isolates holding effect under good flow.	0.90
≥30% (Strong cues)	Extended holding	High	Behavioral delay plus crowding increases exploratory behavior and mis-routing. Tests compounding behavioral stressors.	0.85
15–30% (Moderate cues)	No extended holding	Low	Cue strength sufficient for many fish, but routing errors increase. Moderate straying baseline.	0.85
15–30% (Moderate cues)	Extended holding	Low	Delayed migration reduces homing fidelity under ambiguous cues. Common stress-year scenario.	0.75
15–30% (Moderate cues)	Extended holding	High	Combined delay and density effects overwhelm moderate cues. Compounding straying driver.	0.70
<15% (Weak cues)	No extended holding	Low	Trinity plume weak relative to Klamath; many fish overshoot or remain mainstem. Low-flow straying scenario.	0.70
<15% (Weak cues)	Extended holding	Low	Holding upstream strongly increases straying when cues are weak. High-risk routing conditions.	0.60

Trinity Flow Share at Confluence	Holding Duration	Crowding / Predation Pressure	Biological Interpretation	Combined Entry Survival Multiplier
<15% (Weak cues)	Extended holding	High	Cue failure plus behavioral displacement leads to substantial straying. Worst-case routing scenario for Limiting Factors Analysis testing.	0.55

In River Harvest: In-river harvest is applied as an age-specific removal before holding habitat capacity is evaluated, so harvested fish do not contribute to holding demand or spawning habitat pressure. Harvest represents total in-river removals between Klamath River entry and pre-spawning staging and is applied as a single accounting step. Age-specific rates are derived from PFMC annual reports (Table 4). When run-specific escapement falls below the adjustable thresholds of 8,000 fall-run adults or 4,000 spring-run adults, the harvest rate is reduced to 0.03 (PFMC 2026). These escapement thresholds and the reduced rate are expert-derived values used to represent escapement-dependent harvest management. Unless a threshold is triggered, the same age-specific rates are applied to spring- and fall-run Chinook salmon.

Table 4. Hatchery origin fall-run age-specific in-river harvest rates from PFMC annual reports and survival multiplier.

Age Class	In-river Harvest Rate	Survival Multiplier (1 − h)
Age 2	0.20	0.80
Age 3	0.33	0.66
Age 4	0.33	0.66
Age 5	0.10	0.90

Adult immigration in the Trinity River: The LFA accounts for survival losses in the Trinity River before holding and spawning due to temperature, disease, and dissolved oxygen conditions. The biological mechanisms and categorical structure follow those used for Klamath River adult immigration, but the Trinity-specific temperature categories and combined survival multipliers in Table 5 are expert-derived values because empirical estimates of adult immigration survival under these combined conditions are unavailable for the Trinity River. Therefore, the value of 0.96 was selected to represent approximately 4% mortality under favorable or mildly stressful migration conditions, informed by the documented biological mechanisms and used for calibration and sensitivity testing. Users select one Table 5 condition, and the resulting multiplier is applied to both spring- and fall-run Chinook salmon for the full model run. The survival rate of 0.96 is an expert-derived baseline model assumption.

Table 5. Combined survival multipliers for adult chinook salmon during adult immigration in the Trinity River.

Temperature Bin (≥5–7 Day Exposure)	Disease Condition	Water Quality Condition	Biological Interpretation	Combined Survival Multiplier
≤16 °C	No detectable disease	DO ≥6 mg/L	Near-optimal Trinity migration conditions; little thermal or disease stress. Typical of spring-run entry period but covered by holding habitat quality.	0.99
≤16 °C	Low pathogen presence	DO ≥6 mg/L	Minor disease pressure; little interaction with temperature.	0.96
16–18 °C	No detectable disease	DO ≥6 mg/L	Mild thermal stress; most adults migrate successfully—baseline conditions for both spring-run and fall-run for migration period.	0.96
16–18 °C	Low–moderate pathogen presence	DO ≥6 mg/L	Sublethal stress with early disease amplification.	0.92
18–20 °C	No detectable disease	DO ≥6 mg/L	Elevated metabolic demand; survival reduced but migration possible. Typical of conditions in warm years.	0.90
18–20 °C	Moderate pathogen presence	DO ≥6 mg/L	Disease converts thermal stress into meaningful mortality.	0.80
18–20 °C	Moderate pathogen presence	DO <6 mg/L	Reduced aerobic scope increases residence time and exposure.	0.75
>20 °C	No detectable disease	DO ≥6 mg/L	Sustained thermal stress within Trinity; migration delayed and mortality increases.	0.80
>20 °C	High pathogen presence / epizootic	DO ≥6 mg/L	Warm-water disease outbreaks drive pre-spawn mortality.	0.60
>20 °C	High pathogen presence	DO <6 mg/L	Compounding heat, disease, and hypoxia within the Trinity River.	0.50

Holding in Trinity River (Spring-Run only): Spring-run Chinook salmon entering the Trinity River must hold in cold, deep pool habitats for several months (~ May through September) prior to spawning (Healey 1991). Successful completion of this life stage requires survival and maturation through the holding period without excessive thermal stress, disease exposure, or energetic depletion. Unlike fall-run Chinook salmon, spring-run Chinook salmon are uniquely dependent on holding habitat and are therefore sensitive to habitat capacity, temperature, and spatial distribution. This life stage transition is explicitly capacity-limited and dependent on the

amount of available quality holding habitat with sufficient depth, temperatures, velocity, and cover (Barnhart and Hillemeier 1994; Moyle 2002).

Holding habitat for spring-run Chinook salmon in the Trinity River is evaluated using spatially explicit pool mapping combined with empirically derived volume-based density estimates from a nearby cold-water tailwater system (Clear Creek). A Clear Creek study in 2021 was used as a surrogate for the Trinity River, with densities used to inform capacity from the spatially explicit mapping of holding habitat in the Trinity River (Table 6). Users can adjust the depth, density, and total pool area within the user interface. The model uses a default depth of 1.5 m, density of 0.21 fish/m^3, and 31,746 m^2 for the total area of holding pools in the Trinity River. The application of these densities to the Trinity River, the selection of a default depth threshold of 1.5 m, and the translation of mapped pool habitat into fish capacity represent professional-judgment assumptions adopted to provide a transparent capacity framework for the LFA. The literature supports the biological importance of holding habitat and the use of volumetric capacity concepts, whereas the specific density and capacity assumptions represent the best available surrogate information for evaluating whether summer holding habitat could function as a limiting factor for Trinity River spring-run Chinook salmon.

Table 6. Holding habitat depths and observed densities and translated volume requirements from Clear Creek (unpublished report).

Holding Habitat Depth	Mean Density	Volume Required
≥ 1.5 m	~0.21 fish/m^3	~5.0 m^3/fish
≥ 2.0 m	~0.37 fish/m^3	~3.1 m^3/fish

Holding habitat quantity and capacity are not directly linked to flow. Users can represent flow- or restoration-related changes by adjusting holding habitat area, depth, and fish density. Suitable holding habitat is defined as mapped pool habitat with maximum depth ≥2.0 m, including pool areas ≥1.5 m deep. Holding capacity is calculated as suitable pool area multiplied by selected depth and fish density. Because pool-specific temperature data are unavailable, mainstem Trinity River temperature is used as a proxy for holding conditions. Holding habitat is treated as a hard capacity constraint: adults exceeding capacity experience 100% pre-spawn mortality, while adults within capacity receive the selected temperature-dependent survival multiplier from Table 7. Capacity losses and survival are applied proportionally among age classes. Users select one Table 7 condition, which remains fixed for the full simulation.

Elevated temperatures during the holding period increase physiological stress, disease susceptibility, and pre-spawn mortality risk, while access to cold-water refugia can improve survival and holding success (Strange 2010; Keefer et al. 2018; Isaak et al. 2015). Professional judgment was used to translate these literature-supported biological relationships into a scenario-based life-cycle modeling framework. The temperature categories are based on documented thermal responses of holding adult Chinook salmon, whereas the associated survival multipliers are expert-derived values used to represent increasing thermal stress in the absence of empirical Trinity River holding-survival estimates.

Table 7. Holding habitat capacity and condition survival multipliers.

Holding Habitat Capacity	Holding Habitat Condition	Mainstem Temperature Proxy	Biological Interpretation	Holding Survival Multiplier
Adults > Capacity	Any	Any	Fish displaced from suitable habitat; assumed complete loss.	0.00 (100% mortality)
Adults ≤ Capacity	High-quality holding	≤15.6 °C daily avg (≥50% of days)	Conditions consistent with Clear Creek observations; minimal stress. **This is the baseline condition assumed in the model.**	0.95
	Adequate holding	15.6–17 °C	Mild thermal stress; low pre-spawn mortality.	0.90
	Marginal holding	17–18 °C	Elevated metabolic demand; increased disease risk.	0.85
	Thermally stressed holding	18–20 °C	Sustained stress reduces fitness and survival.	0.75
	Severe thermal stress	>20 °C	Holding success unlikely even for fish within capacity.	0.60

Adult spawning in the Trinity River: This transition evaluates adult spawning in the Trinity River by explicitly linking spawning habitat capacity to the age- and sex-specific composition of returning adults. Adults surviving migration and, for spring-run fish, the holding period are first partitioned by age-specific sex ratios, reflecting the strong male bias at younger ages and near parity among older adults (Table 8). Because only females construct redds and require spawning territory, spawning habitat demand is calculated as the age-weighted sum of female space requirements, where required area per female increases with body size and age through established redd size and inter-redd spacing relationships. Typical female sizes at age were based on Trinity data, and redd area was calculated as $0.0006 \times \text{length}^2$ with territory (4 x redd area) from Burner (1951) (Table 9).

Table 8. Age-specific sex ratios for returning adult, with run-specific proportions derived from Trinity River Hatchery returns.

Age Class	Proportion Females	Proportion Females (Fall-Run)	Proportion Females (Spring-Run)	Rationale
Age 2	0.01	0.01	0.01	Jacks are predominantly male; female jacks (jills) are rare but not impossible.
Age 3	0.44	0.43	0.48	First major female maturation age, assumed to be slightly below parity.
Age 4	0.58	0.44	0.58	Near parity typical.
Age 5	0.52	0.59	0.47	Slight female bias plausible due to delayed maturation.

Table 9. Age-specific female size, redd area as a function of female size, and effective territory used to estimate required redd capacity.

Age Class	Typical Female Fork Length (cm)	Redd Area per Female (m²)	Effective Territory per Female (m²)	Interpretation for Spawning Capacity
Age 2	~49	~1.4	~5.8	Small females; rare contributors to total spawning demand.
Age 3	~66	~2.6	~10.5	Moderate redd size; first major female spawning age. *Note: Modeled hatchery fish use this logic.*
Age 4	~78	~3.7	~14.6	Large, highly fecund females with substantial space demands.
Age 5	~83	~4.1	~16.5	Largest females; highest per-capita impact on capacity.

Spring- and fall-run Chinook salmon are modeled separately through adult immigration and holding but are combined after spawning because introgression blurs genetic distinctions and subsequent monitoring cannot reliably assign offspring to run type (Thompson et al. 2020).

Total female spawning demand is compared with mapped suitable spawning habitat. Habitat occupied by naturally spawning hatchery-origin females is removed first. If natural-origin female demand exceeds the remaining habitat, only the number of females that can be accommodated are treated as effective spawners. The model does not include a density-dependent superimposition function; females exceeding capacity do not contribute eggs. This hard cutoff is an expert-derived simplification used to test spawning-habitat capacity with available data.

For spawning habitat, we consider three reaches:

- **Reach 1:** (Lewiston Hatchery to Old Lewiston Bridge / Bucktail) — the upper 10.9 km below Lewiston Dam (hatchery-influence zone).
- **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 amount of spawning habitat in each reach was derived from S3 spawning-habitat output. Because S3 output was considered an overestimate of effective spawning capacity according to TRRP participants, total habitat was reduced during model tuning until spawning demand began to interact with available habitat. The final default capacities remain uncertain and are treated as expert-derived values for calibration and sensitivity testing. The proportion of hatchery-origin spawners among reaches follows the spatial pattern in coded-wire-tag spawned-female recoveries: most hatchery-origin spawners occurred within 10 km of Trinity River Hatchery, few occurred in the middle reaches, and none were predicted below Del Loma in most years. Hatchery-origin spawners are set by an adjustable proportion of total spawning adults, with a default of 20% and a maximum of 570 naturally spawning hatchery-origin adults (Gough et al. 2024).

The model explicitly considers the contribution of hatchery-origin adults to spawning habitat demand, recognizing that hatchery and natural-origin spawners compete for the same physical spawning habitat. Hatchery-origin females are included fully in redd demand calculations and

therefore influence whether spawning habitat capacity is exceeded, without assuming differences in per-redd productivity or imposing density-dependent superimposition functions. The model assumes a default proportion of hatchery-origin females from the total Trinity escapement by reach based on data reported primarily in Gough et al. (2024) (Table 10), and a default age 3 (to determine redd size) for HOS to reduce redd capacity for natural-origin spawners. The proportion of hatchery-origin spawners assigned to each reach (0.82, 0.18, and 0.00) was developed using professional judgment to translate the observed spatial pattern into a tractable life-cycle modeling framework.

Spawning habitat was estimated from S3 output using Pear Tree daily flows for the September to December spawning season during 2005 to 2025. The 5th, 25th, 50th, 75th, and 95th percentile flows were 340, 414, 490, 597, and 1,340 cfs, respectively. Mesohabitat unit 351, corresponding to the Pear Tree gauge, was matched to the nearest S3 flow groups: 342, 410, 492, 594, and 1,341 cfs.

Model reaches were defined by S3 mesohabitat units: 1 through 50 (Reach 1), 51 through 354 (Reach 2), and 355 through 910 (Reach 3). For each flow, spawning habitat was summed by reach and across the river. Reach proportions were consistent among flows, averaging 10%, 40%, and 50% in Reaches 1, 2, and 3, respectively (Table 11). The LCM therefore allocates total spawning habitat using this fixed 10/40/50 split (Table 10).

During tuning and calibration, total spawning habitat was initially set high enough to avoid capacity limitation and then reduced until the population began interacting with available habitat; the 10/40/50 reach allocation remained fixed.

Spawning habitat is allocated from upstream to downstream. Within each reach, available habitat is distributed among age classes in proportion to female abundance. If total spawning demand is less than available habitat, all females spawn. If demand exceeds capacity, habitat is filled sequentially from Reach 1 through Reach 3, and females remaining after all available habitat is occupied do not spawn. This upstream-first allocation is an expert-derived simplification used to represent preferential use of upstream spawning habitat.

Table 10. Summary of spawning activity by reach that are used to inform spawning capacities and spatial distribution of spawning activity. The table includes model reach length and hatchery origin spawners breakdown by reach. This is not saying that 82% of the habitat in reach 1 is used by hatchery-origin spawners, rather 82% of the hatchery origin spawners use reach 1.

Model Reach	Length (km)	Spawning Capacity (m^2)	Proportion of Hatchery Origin Spawners Among Reaches (default)
1	10.6	35,000	0.82
2	54.2	140,000	0.18
3	117.4	175,000	0.00

Table 11. Summary of spawning capacity from S3 based on flow from the Pear Tree USGS gauge.

Model Reach	Length (km)	S3 Spawning Capacity (5th Percentile)	S3 Spawning Capacity (25th Percentile)	S3 Spawning Capacity (Median Flow)	S3 Spawning Capacity (75th Percentile)	S3 Spawning Capacity (95th Percentile)
1	10.6	90,578 m^2	94,957 m^2	96,475 m^2	97,681 m^2	105,602 m^2

Model Reach	Length (km)	S3 Spawning Capacity (5th Percentile)	S3 Spawning Capacity (25th Percentile)	S3 Spawning Capacity (Median Flow)	S3 Spawning Capacity (75th Percentile)	S3 Spawning Capacity (95th Percentile)
2	54.2	437,117 m^2	448,024 m^2	460,652 m^2	472,199 m^2	488,122 m^2
3	117.4	539,346 m^2	561,994 m^2	586,847 m^2	618,417 m^2	714,863 m^2

LFA Rules and Model Logic Overview

The following section provides an overview of the model logic (Steps) that feed into the LFA testing described in the next section. Following these steps below, we take the abundance of adults by run type and age classes entering the Klamath River from the previous life stage transition and move them through the Klamath River to entry into the Trinity River and ending with the construction of redds (the abundance used for the next life stage transition).

STEP 1: Klamath Temperature, Disease, and Water-Quality Survival

Inputs: Abundance of adults by run type and age classes at Klamath River entry.

Calculation(s): Multiply starting abundance of adults by combined temperature, disease, and water quality survival multiplier – with baseline values for both spring-run and fall-run Chinook salmon (Table 2).

Outputs: Abundance of immigrants by run type and age class that survive adult immigration to Trinity River confluence.

STEP 2: Trinity Confluence Routing (Straying, holding and crowding)

Inputs: Abundance of adults by run type and age class surviving adult immigration through the Klamath River to Trinity River mouth.

Calculation(s): Multiply abundance by combined survival multipliers based on flow split, confluence holding, and crowding (Table 3) – note baseline values are shown in table. This effectively treats straying as an additional hit on survival since it removes adults from the returning population to the Trinity River.

Outputs: Abundance of adults by run type and age class that survive or make it into the Trinity River.

STEP 3: Straying into Trinity River

Inputs: Abundance of adults by run type and age class that survive or make it into the Trinity River.

Calculation(s): Based on the selected Klamath-origin straying proportion, calculate the number of additional fish entering the Trinity River using Trinity escapement for the current model year as the scaling abundance. Allocate these fish proportionally among run types and age classes, then add them to Trinity River entry abundance.

Output: Abundance of fish entering the Trinity River by run type and age class, including fish that stray into the Trinity River.

STEP 4: In-river harvest

Inputs: Abundance of adults by run type and age class entering the Trinity River after Trinity confluence routing and addition of Klamath-origin strays from Step 3.

Calculation(s): Multiply abundance by run type by age-specific in-river harvest rates from Table 4. If the abundance is below a given threshold, the in-river harvest rate will be reduced to 0.003. Calculated separately for each run.

Outputs: Abundance of adults by run type and age class after in-river harvest is accounted for.

STEP 5: Trinity River adult immigration survival

Inputs: Abundance of spring-run and abundance of fall-run adults that successfully entered the Trinity River after harvest is accounted for (from Step 4).

Calculation(s): Multiply abundances by combined survival multipliers based on temperature, disease, and dissolved oxygen multipliers (Table 5).

Outputs: Abundance of spring- and fall-run adults by age class that survive adult immigration in the Trinity River.

For spring-run Chinook salmon, proceed to Step 6;

For fall-run Chinook salmon, proceed to Step 8.

STEP 6: Holding habitat capacity filter (Spring-Run only)

Inputs: Abundance of spring-run adults **ONLY** by age class from Step 5, holding habitat area, depth, and fish density (Table 6).

Calculation(s): Compare the holding capacity to spring-run adult abundance:

- IF abundance < holding capacity, then all spring-run adults proceed to Step 7.
- IF abundance > holding capacity, then all adults in excess of holding capacity get 100% mortality (applied proportionally across age classes) and all adults within holding capacity are moved to Step 7.

Outputs: Abundance of spring-run adults by age-class within the holding habitat capacity.

STEP 7: Holding habitat survival (Spring-Run only)

Inputs: Abundance of spring-run adults by age-class from Step 6.

Calculation(s): Multiply the abundance of spring-run adults by age classes by survival multipliers based on holding habitat condition and temperature (Table 7).

Outputs: Abundance of spring-run adults by age class that survive holding in Trinity River until spawning.

STEP 8: Allocate adults to females by age class

Inputs: Abundance of adults by age class from Step 7 (spring-run) and Step 5 (fall-run), and abundance of hatchery-origin females by age class.

Calculation(s): Multiply abundance by age class by proportion females from Table 8.

Outputs: Abundance of female spawners by origin, and age class.

STEP 9: Calculate total spawning habitat demand

Inputs: Abundance of females by origin and age class from Step 8.

Calculation(s): Multiply female abundance by age class by age-specific size, redd area, and territory to derive space requirements (Table 9). Hatchery origin fish utilize age 3 territory requirements.

Outputs: Total space requirement to construct and defend redds by origin and age class, used to compare to spawning habitat area.

STEP 10: Compare spawning habitat demand to available habitat

Inputs: Total spawning habitat area demand from Step 9 and available spawning habitat area.

Calculation(s): From the total available spawning habitat, remove the amount utilized by hatchery-origin fish (Table 10). Compare the remaining available spawning habitat area to spawning habitat demand from Step 9 for natural fish.

- IF abundance < spawning habitat capacity, then all redds advance to next life stage transition.
- IF abundance > spawning habitat capacity, then only the redds up to the spawning habitat capacity are advanced to the next life stage (all other redds in excess of spawning capacity are removed proportional to age class abundance).

Redds are allocated from upstream to downstream, with available habitat within each reach distributed among age classes in proportion to female abundance, until all habitat is occupied or all females have spawned.

Outputs: Total redds that advance to the next life stage.

Conceptual Basis for LFA Testing:

The following LFA Tests evaluate whether limitations on adult Chinook salmon abundance and successful reproduction occur during adult immigration through the Klamath River, entry into the Trinity River, spring-run holding, or spawning in the Trinity River. Tests are structured to sequentially relax individual constraints and evaluate whether improvements plausibly close the gap between observed and desired escapement or redd abundance. Similar to other LFA tests, we rely primarily on recovery targets to evaluate and classify limiting factors as primary limiting factors (alone sufficient to explain the shortfall), a compounding limiting factor (important only in combination), or non-limiting (present but not constraining outcomes) with respect to adult Chinook salmon returns to the Trinity River.

Fall-run Chinook Salmon Targets:

1. Increase escapement of naturally-produced fall-run Chinook salmon to 62,000.
2. Population supports harvest (across all sectors) of 131,750 adults.

Spring-run Chinook Salmon Targets:

1. Increase escapement of naturally-produced spring-run Chinook salmon to 6,000.
2. Population supports harvest (across all sectors) of 12,750 adults.

Test 1: Are Adult immigration and routing the primary limiting factor on Trinity River spawner abundance?

Hypothesis: Adult abundance on Trinity River holding and spawning grounds is primarily limited by mortality during adult immigration through the Klamath and Trinity rivers and by routing losses at the Trinity River confluence.

Approach: Apply incrementally more favorable adult immigration conditions for: Klamath River adult immigration survival, Trinity River adult immigration survival, holding habitat survival, and strong Trinity confluence cues (≥30% Trinity flow share, minimal upstream holding; straying survival) while holding in-river harvest, holding habitat capacity, and spawning habitat capacity at baseline levels. If adult immigration survival or routing is limiting, then improving survival and entry alone should substantially increase adult abundance reaching Trinity River habitats, resulting in an overall increase in adult escapement.

Diagnostics and Interpretation:

1. Adult abundance at Trinity holding/spawning habitat remains low under favorable adult immigration and routing conditions → Limitation must occur elsewhere in the life cycle (e.g., holding habitat, spawning habitat, or earlier stages).
2. Adult abundance at Trinity holding/spawning habitat increases substantially and approaches recovery targets → Adult immigration survival and/or routing losses are a primary limiting factor on spawner abundance.

Management Interpretation:

This test distinguishes whether recovery is fundamentally constrained by processes occurring outside Trinity River management influence (adult immigration and routing) or whether

Trinity-focused actions alone could plausibly achieve recovery targets once downstream constraints are alleviated.

Test 2: Is spring-run holding habitat the primary limiting factor on Trinity River spawner abundance?

Hypothesis: Spring-run Chinook salmon escapement to Trinity River spawning grounds is primarily limited by the capacity and thermal suitability of available holding habitat, such that spring-run adult abundance surviving to spawning cannot exceed the maximum number of adults that can be accommodated within existing holding habitat under current conditions.

Approach: Apply post-immigration, post-routing spring-run adult abundance entering the Trinity River. Hold adult immigration survival and confluence routing at baseline conditions and evaluate both baseline in-river harvest and a zero-harvest scenario. Apply holding habitat capacity as a hard biological constraint such that adults in excess of available holding habitat experience 100% pre-spawn mortality, while adults within capacity are subject to temperature-dependent holding survival.

Under these conditions:

- Incrementally increase holding habitat volume (e.g., +100%, +200%) to identify the level of habitat expansion required to achieve the recovery target and to determine whether a new limiting factor emerges once holding constraints are relieved.

This test isolates holding habitat capacity and condition as the potential constraint after adult immigration and routing losses are relaxed.

Diagnostics and Interpretation:

1. Escapement plateaus at a fixed abundance (below the recovery target) under current holding habitat volume → Holding habitat is a primary limiting factor that sets an upper biological ceiling on recovery.
2. Escapement increases and approaches recovery targets only after holding habitat volume is increased → Holding habitat quantity is constraining recovery, and habitat expansion is necessary to achieve targets.
3. Holding capacity is rarely exceeded across plausible return levels, and escapement approaches recovery targets without habitat expansion → Holding habitat is not limiting under current conditions, and limitations must occur elsewhere in the life cycle.

Management Interpretation:

This test determines whether recovery is fundamentally constrained by a Trinity-managed habitat bottleneck even under favorable downstream conditions. If holding habitat sets a hard ceiling on escapement, then improvements to downstream survival or harvest reductions alone will be insufficient to achieve recovery targets without holding habitat expansion or temperature management. Conversely, if holding habitat does not emerge as limiting, restoration and management actions should focus on other life-stage transitions within or outside the Trinity Basin.

Test 3: Is spawning habitat limiting once age, sex, and origin composition are accounted for?

Hypothesis: Adult Chinook salmon escapement to Trinity River spawning is primarily limited by the availability of suitable spawning habitat once age-specific sex ratios and hatchery-origin spawners are accounted for, such that total female spawning demand exceeds available spawning habitat area under plausible adult return levels.

Approach: Use post-harvest, post-migration (and post-holding for spring-run) adult abundance entering the spawning stage for spring- and fall-run Chinook salmon combined. Allocate adults to females using age-specific sex ratios and partition spawners by natural- and hatchery-origin components.

Compute total spawning habitat demand as the sum of age-specific female redd area and effective territory requirements for all natural females. Compare total demand to mapped spawning habitat area using a hard capacity cutoff (i.e., no density-dependent superimposition function).

Under this structure:

- Incrementally reduce spawning habitat to evaluate whether and when female spawning demand exceeds available habitat and how that impacts escapement. Do this with and without ocean and in-river harvest impacts.
- Evaluate spawning capacity under different hatchery-origin spawner assumptions to isolate the role of hatchery females as a compounding constraint. Adjust the proportion of hatchery females allotted to each spawning reach.

This test explicitly evaluates spawning habitat limitation only after adult immigration, routing, harvest, and holding constraints have already been applied and held fixed.

Diagnostics and Interpretation:

1. Spawning demand exceeds capacity regardless of hatchery contribution → Spawning habitat is a primary limiting factor due to structural insufficiency.
2. Spawning demand rarely approaches capacity despite low escapement → Spawning habitat is not limiting under current conditions; constraints must occur earlier in the life cycle.

These diagnostics distinguish physical habitat limitation from spawner composition effects.

Management Interpretation:

This test determines whether recovery of natural Chinook salmon production is constrained by physical spawning habitat availability or by competition introduced through hatchery-origin spawners. If spawning habitat capacity is exceeded only when hatchery females are present, hatchery management actions may alleviate constraints without habitat expansion. If capacity is exceeded regardless of origin, spawning habitat restoration or flow-dependent habitat improvements would be required to support higher escapement.

Test 4: Where does the bottleneck occur under best-plausible conditions?

Hypothesis: If downstream and anthropogenic constraints are removed, the primary bottleneck limiting Chinook salmon recovery will shift into Trinity-managed habitats, revealing either holding habitat (spring-run) or spawning habitat as the dominant remaining constraint on escapement.

Approach: Simultaneously apply upper-bound plausible conditions for:

- Adult immigration survival in the Klamath and Trinity rivers,
- Strong Trinity River confluence cues (≥30% Trinity flow share, minimal holding),
- Zero or minimal in-river harvest.

Under these favorable conditions, sequentially evaluate:

1. Holding habitat capacity and holding survival for spring-run Chinook salmon, and
2. Spawning habitat capacity for combined spring- and fall-run Chinook salmon, and
3. Rearing habitat capacity for Trinity River juvenile outmigrants.

Run the test where all three capacities are reduced collectively and individually by 10, 25, and 50%. All downstream constraints are relaxed simultaneously so that Trinity-managed habitats are examined as the next potential limiting factors. This test does not isolate individual mechanisms; rather, it synthesizes Tests 1 through 3 to identify which constraint becomes binding once others are removed.

Diagnostics and Interpretation:

1. Escapement increases until holding capacity is reached → Holding habitat is the dominant Trinity-managed bottleneck; recovery requires holding habitat expansion or improved thermal conditions.
2. Escapement increases through holding but plateaus at spawning capacity → Spawning habitat is the dominant Trinity-managed bottleneck.
3. Escapement increases through holding and spawning but plateaus at rearing capacity → Rearing habitat is the dominant Trinity-managed bottleneck.
4. Escapement remains well below recovery targets despite relaxed conditions → Limiting factors remain downstream of Trinity management influence.

These diagnostics distinguish physical habitat limitation from spawner composition effects.

Management Interpretation:

This is a key diagnostic test that identifies whether Chinook salmon recovery constraints are resolvable through Trinity River management actions alone. By revealing the first binding constraint under best-plausible conditions, this test guides prioritization among holding habitat restoration, spawning habitat enhancement, or actions outside the Trinity Basin necessary to achieve recovery targets.

References

Barnhart, R. A., and D. C. Hillemeier. 1994. Summer habitat utilization by adult spring Chinook salmon and summer steelhead, South Fork Trinity River, California. California Cooperative Fishery Research Unit, Humboldt State University, Arcata, California.

Bartholomew, J. L., J. D. Alexander, S. L. Hallett, G. Alama-Bermejo, and S. D. Atkinson. 2022. Ceratonova shasta: a cnidarian parasite of annelids and salmonids. Parasitology 149:1862–1875.

Burner, C. J. 1951. Characteristics of spawning nests of Columbia River salmon. Fishery Bulletin of the Fish and Wildlife Service 61:93–100.

De Jong, H. W. and T. J. Mills. 1992. Anadromous salmonid escapement studies, South Fork Trinity River, 1984–1990. California Department of Fish and Game, Inland Fisheries Administrative Report 92, Sacramento, California. Available: https://www.krisweb.com/biblio/sft_cdfg_jong_1992_escapment/jong.htm. (April 2026).

Gough, S. A., R. Smit, K. Lindke, K. De Juilio, C. Laskodi, G. Kautsky, and B. C. Matilton. 2024. Assessment of adult salmonid spawning in the Trinity River. Arcata Fish and Wildlife Office Technical Report TR-2024-71. U.S. Fish and Wildlife Service.

Hamilton, S. A. and D. D. Murphy. 2018. Analysis of limiting factors across the life cycle of delta smelt (*Hypomesus transpacificus*). Environmental Management 62(2):365–382.

Healey, M. C. 1991. Life history of Chinook salmon (Oncorhynchus tshawytscha). Pages 311–394 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Isaak, D. J., and M. K. Young. 2023. Cold-water habitats, climate refugia, and their utility for conserving salmonid fishes. Canadian Journal of Fisheries and Aquatic Sciences 80:1187–1206.

Isaak, D. J., M. K. Young, D. E. Nagel, D. L. Horan, and M. C. Groce. 2015. The cold-water climate shield: delineating refugia for preserving salmonid fishes through the 21st century. Global Change Biology 21:2540–2553.

Keefer, M. L., C. C. Caudill, C. A. Peery, and T. C. Bjornn. 2006. Route selection in a large river during the homing migration of Chinook salmon (Oncorhynchus tshawytscha). Canadian Journal of Fisheries and Aquatic Sciences 63:1752–1762.

Keefer, M. L., T. S. Clabough, M. A. Jepson, E. L. Johnson, C. A. Peery, and C. C. Caudill. 2018. Thermal exposure of adult Chinook salmon and steelhead: diverse behavioral strategies in a large and warming river system. PLoS ONE 13:e0204274.

Keefer, M. L., and C. C. Caudill. 2014. Homing and straying by anadromous salmonids: a review of mechanisms and rates. Reviews in Fish Biology and Fisheries 24:333–368.

Moyle, P. B. 2002. Inland fishes of California, revised and expanded edition. University of California Press, Berkeley.

Regional Mark Processing Center (RMPC). 2026. Coded-wire tag information system. Pacific States Marine Fisheries Commission. Available: https://www.rmpc.org/resources/cwt-info/. (April 2026).

Robinson, H. E., J. D. Alexander, J. L. Bartholomew, S. L. Hallett, N. J. Hetrick, R. W. Perry, and N. A. Som. 2022. Using a mechanistic framework to model the density of an aquatic parasite, Ceratonova shasta. PeerJ 10:e13183.

Snyder, M. N., N. H. Schumaker, J. B. Dunham, J. L. Ebersole, M. L. Keefer, J. Halama, R. L. Comeleo, P. Leinenbach, A. Brookes, B. Cope, and J. Wu. 2022. Tough places and safe spaces: can refuges save salmon from a warming climate? Ecosphere 13:e04265.

Strange, J. S. 2010. Summary of scientific evidence to guide special flow releases to reduce the risk of adult fall Chinook salmon mass disease mortality in the lower Klamath River. Trinity River Restoration Program, Weaverville, California. Available: https://www.trrp.net. (April 2026).

Strange, J. S. 2012. Migration strategies of adult Chinook salmon runs in response to diverse environmental conditions in the Klamath River basin. Transactions of the American Fisheries Society 141:1622–1636.

Thompson, N. F., E. C. Anderson, A. J. Clemento, E. Campbell, D. E. Pearse, J. W. Hearsey, A. P. Kinziger, and J. C. Garza. 2020. A complex phenotype in salmon controlled by a simple change in migratory timing. Science 370:609–613.

Westley, P. A. H., T. P. Quinn, and A. H. Dittman. 2013. Rates of straying by hatchery-produced Pacific salmon (*Oncorhynchus* spp.) and steelhead (*Oncorhynchus mykiss*) differ among species, life history types, and populations. Canadian Journal of Fisheries and Aquatic Sciences 70(5):735–746.

INCUBATION TO EMERGENCE:

Description of Life Stage Transition:

This life-stage transition represents the survival of fertilized Chinook salmon eggs (embryos) from deposition in completed redds through incubation and emergence as free-swimming fry. The transition begins with effective redds constructed during spawning (as determined in the previous life stages) and ends when fry emerge from the gravel, becoming available to subsequent rearing life stages. Unlike adult migration or holding, this life stage is not constrained by habitat capacity, but rather by per-redd viability, which is governed by interactions between spawning habitat quality, hydrologic and thermal conditions during incubation, maternal condition, and female size and age structure. Because embryos and alevin are effectively immobile throughout incubation, survival during this period is highly sensitive to local gravel composition, flow stability, incubation temperature, nutrient provisioning to embryos, and the ability of females of different sizes to successfully construct and protect redds. Because multiple independent mechanisms operate concurrently during incubation, egg-to-emergence survival is modeled as a sequence of multiplicative survival filters applied at the redd and egg scale, allowing the LFA to diagnose which environmental or biological factors most strongly limit early life-stage production. Some of the considered factors are linked to parentage and set the stage for survival, while others are modeled as acting on embryo survival during the incubation period.

- Female age and size (maternal effects)
- Redd construction success (female size × gravel size interaction)
- Spawning gravel quality (fine sediment content)
- Hydrologic disturbance during incubation
- Incubation temperature
- Thiamine deficiency (maternal nutrient limitation)
- Spawner origin (compounding effect of hatchery origin fitness)

Assumptions for LFA and LCM Rules:

Fecundity and egg deposition: This step converts effective spawning females into incubating eggs using age- and size-specific fecundity relationships (Healey and Heard 1984). Larger and older Chinook salmon females produce more eggs than younger females, with fecundity generally ranging from ~2,500 to more than 5,000 eggs per female (Table 12; Healey and Heard 1984; Ohlberger et al. 2020). Hatchery-origin females that spawn naturally receive a 0.5 multiplier to represent reduced reproductive success and egg-to-fry survival. Recent declines in female body size are associated with lower egg production per female, making age and size structure directly relevant to early life-stage production (Heath et al. 2003; Gallinat and Chang 2013; Ohlberger et al. 2020; Iritani et al. 2025). The model includes age-specific fecundity scalars and adjustable inputs for naturally spawning hatchery-origin fish.

Table 12. Age-specific female size from Trinity River Hatchery returns and fecundity for Chinook salmon (Healey and Heard 1984).

Age Class	Typical Female Fork Length (cm)	Approximate Body Size Class	Typical Fecundity (eggs/female)	Relative Egg Production	Interpretation for LFA
Age 2	~49	Small ("jill")	~2,461	Low	Minor contributor to total egg pool; highly sensitive to gravel and incubation conditions.
Age 3	~66	Medium	~3,712	Moderate	First major contributor to egg production; affected by both habitat and size structure.
Age 4	~78	Large	~4,674	High	Disproportionately important for total egg and fry production.
Age 5	~83	Very large	~5,093	Very high	Small proportion of spawners can dominate egg output and buffer poor conditions.
Hatchery origin	~49-83	Ranges	~3,712	Moderate	

Redd construction success (Female Size × Gravel Size Constraint): This step evaluates whether females of a given size can successfully excavate functional redds in the available spawning gravel. Empirical and mechanistic evidence indicates that a female Chinook salmon can only mobilize gravel ~ 10% of her body length; if characteristic gravel size (e.g., D_{84}) exceeds this threshold, redd construction fails, and results in egg survival for that female being effectively zero. External literature supports the 10% body-length rule and the direction of the female size–gravel relationship (Table 13; Burner 1951; Reiser and Bjornn 1979; Kondolf and Wolman 1993). The 0.5 marginal-excavation value is an expert-derived value for partial redd construction near the upper movable-gravel limit. This mechanism disproportionately affects younger, smaller females and directly links gravel size distributions to survival from redd construction to emergence.

The characteristic gravel size is set for each reach to reflect potential reach-level spatial variation in substrate characteristics. In the model, the baseline gravel was set to ≤5 cm for each reach, resulting in a redd multiplier of 1.00 for each age. The exact 0.5 marginal multiplier and cutoff ranges are expert-judgment assumptions used to translate the biological mechanism into scenario-based LFA model inputs.

Table 13. Age-specific female sizes and redd construction survival multipliers by substrate size classifications.

Female Age Class	Typical Approximate Female Fork Length (cm)	Max Movable Gravel (cm) (≈ 0.10 × Length)	Characteristic Gravel Size (D84, cm)	Redd Construction Outcome	Redd Construction Survival Multiplier
Age 2	49	4.9	≤5	Can excavate redd. **Baseline.**	1.0
Age 2	49	4.9	5–6.5	Marginal / partial excavation.	0.5
Age 2	49	4.9	>6.5	Cannot excavate redd.	0.0
Age 3	66	6.6	≤6.5	Can excavate redd. **Baseline.**	1.0
Age 3	66	6.6	6.5–8	Marginal / partial excavation.	0.5
Age 3	66	6.6	>8	Cannot excavate redd.	0.0
Age 4	78	7.8	≤8	Can excavate redd. **Baseline.**	1.0
Age 4	78	7.8	8–9.5	Marginal / partial excavation.	0.5
Age 4	78	7.8	>9.5	Cannot excavate redd.	0.0
Age 5	83	8.3	≤9	Can excavate redd. **Baseline.**	1.0
Age 5	83	8.3	9–10.5	Marginal / partial excavation.	0.5
Age 5	83	8.3	>10.5	Cannot excavate redd.	0.0

Female Size–Dependent Egg Quality and Provisioning: Egg viability is modified to reflect size- and age-dependent maternal provisioning (Beacham and Murray 1990). Older and larger females produce eggs with greater lipid and nutrient content and larger egg size, which supports higher survival potential and results in larger, more robust fry at emergence (Beacham and Murray 1990; Ohlberger et al. 2020). While egg size alone does not guarantee survival, provisioning effects act as a multiplicative viability modifier across all subsequent incubation processes, and we include size-based egg quality survival multipliers for each age class (Table 14). External literature supports the maternal-effect that larger, older females generally produce better-provisioned eggs and larger emergent fry. The age-specific multipliers express relative

egg-quality differences and are expert-derived values rather than directly estimated survival rates.

Table 14. Age- and size-specific survival multipliers for eggs based on female size.

Female Age Class	Typical Approximate Female Fork Length (cm)	Egg Quality / Provisioning Category	Biological Interpretation	Egg Quality Survival Multiplier
Age 2	49	Low	Small eggs, reduced provisioning, shallow nests; fry emerge smaller and less resilient	0.80
Age 3	66	Moderate	Average egg size and provisioning; baseline early survival	0.85
Age 4	78	High	Large eggs, strong provisioning; larger fry at emergence	0.90
Age 5	83	Very high	Highest egg investment and buffering against stress	1.00

Thiamine deficiency (maternal nutrient limitation): This step applies survival penalties associated with thiamine deficiency complex (TDC), a maternal effect linked to adult diet history (Fisher et al. 1995; Fitzsimons et al. 2007; Mantua et al. 2025). Low egg thiamine concentrations cause high mortality late in incubation and during emergence, with LC_{50} values commonly reported near 2.7 nmol/g (Fisher et al. 1995; Fitzsimons et al. 2007). Sub-lethal impairment in surviving fry (e.g., abnormal swimming behavior) further reduces effective recruitment (Brown et al. 2005). Thiamine effects are modeled as an independent, multiplicative survival filter acting near the end of incubation (Table 15). We acknowledge that exposure to diet conditions that would influence thiamine could vary among run types and age classes based on the ocean conditions experienced. For this model application, this will be customizable for age class with a range from 0.00 to 1.00.

The LC_{50} of ~2.7 nmol/g reported from the literature provides the breakpoint for severe thiamine deficiency. Because comparable thresholds are not available for the other categories, we used expert-derived values to define a graded response from no deficiency to near-complete reproductive failure.

Table 15. Thiamine deficiency categories and corresponding survival multipliers.

Egg Thiamine Concentration (nmol/g)	Thiamine Condition Category	Biological Interpretation	Egg-to-Emergence Survival Multiplier
> 7.7	No deficiency	Adequate thiamine stores; normal embryonic development. **Default value.**	1.00
5.9–7.7	Mild deficiency	Slight impairment; modest increase in developmental abnormalities.	0.85

Egg Thiamine Concentration (nmol/g)	Thiamine Condition Category	Biological Interpretation	Egg-to-Emergence Survival Multiplier
2.7–5.9	Moderate deficiency	Clear TDC symptoms in a substantial fraction of eggs/families.	0.60
≤ 2.7	Severe deficiency (LC_{50} range)	High late-stage mortality; many fry fail to hatch or emerge.	0.40
≤ 2.0	Critical deficiency	Near-complete mortality; functional reproductive failure.	0.01

Fine Sediment Effects on Incubation Survival: This step applies survival penalties associated with fine sediment in spawning gravels, a key potential indicator of chronic watershed disturbance in the Trinity River (Krause et al. 2010; Buxton 2021). Elevated fine sediment reduces permeability and interstitial oxygen delivery, substantially lowering embryo survival. Laboratory and field synthesis demonstrates that fine sediment content can explain 90 to 93% of variability in Chinook salmon egg-to-emergence survival, making it one of the strongest mechanistic controls on this life stage (Tappel and Bjornn 1983; Wu 2000). Survival is represented using the Tappel and Bjornn (1983) gravel–fines relationship (Table 16). Note that the sediment conditions are selected independently for each model reach prior to running the model and remain static throughout the model run.

Table 16. Survival multipliers for eggs based on sediment condition.

Fine Sediment Condition	Indicative % Fines (<6.35 mm or <0.85 mm)	Sediment Condition Category	Biological Interpretation	Egg-to-Emergence Survival Multiplier
Low fines	≤10–12%	Clean / well-sorted gravel	High permeability and oxygen delivery; near-optimal incubation. **Default.**	0.95 and 1.00[a]
Moderate fines	~12–15%	Acceptable but impaired	Reduced interstitial flow; moderate embryo stress.	0.80
High fines	~15–20%	Degraded gravel	Strong oxygen limitation; high embryo mortality.	0.40
Very high fines	>20–25%	Severely degraded	Gravel matrix largely clogged; embryo survival very low.	0.10
Extreme fines	>30%	Functionally unsuitable	Redds effectively smothered; near-complete egg loss.	0.01

[a] Baseline conditions use 0.95 for Reach 1 and 1.00 for Reaches 2 and 3.

Hydrologic disturbance during incubation: This step accounts for mortality from scour, burial, or dewatering caused by unstable flows during incubation. High flows can scour redds and displace eggs, while rapid stage reductions can strand incubating embryos. Empirical studies indicate that egg survival decreases by ~16 to 17% for every centimeter increase in substrate

scour depth, underscoring the sensitivity of incubating eggs to flow regime and channel stability (Table 17; DeVries 1997; Montgomery et al. 1996; Montgomery et al. 1999; Beechie et al. 2008). These effects can be treated as event-based or scenario-based penalties, but here we would use higher disturbance categories to represent repeat disturbance events. As with the sediment classification, the hydraulic conditions are selected independently for each model reach and remain static for the duration of the model run.

External literature supports the mechanism that scour, burial, bed mobility, and dewatering reduce egg survival, especially when disturbance approaches egg-pocket depth. Table 17 converts that mechanism into scenario multipliers using expert-derived values.

Table 17. Egg survival multipliers based on hydrological disturbances during incubation.

Hydrologic Condition During Incubation	Indicative Physical Signal	Disturbance Category	Biological Interpretation	Egg-to-Emergence Survival Multiplier
Stable incubation conditions	No mobilizing flows; gradual stage changes	Stable	Redds remain intact; little egg displacement	0.95-1.00[a]
Minor disturbance	Small bed mobility; shallow scour (<1 cm)	Low disturbance	Slight redd rearrangement; modest egg loss	0.90
Moderate disturbance	Partial redd scour (1–2 cm); gravel loosening	Moderate disturbance	Noticeable egg loss; reduced oxygen delivery	0.65
Severe disturbance	Deep redd scour (>2 cm); bed mobilization	High disturbance	Large proportion of eggs displaced or destroyed	0.40
Extreme disturbance	Full redd destruction, burial, or dewatering	Failure	Redds functionally lost; near-complete egg mortality	0.01

[a] Baseline conditions use 0.95 for Reach 1 and 1.00 for Reaches 2 and 3.

Temperature-dependent incubation survival: Incubation temperature influences development rate, metabolic demand, and vulnerability to other stressors such as low oxygen and fine sediment (Alderdice and Velsen 1978; Beacham and Murray 1990). Sustained exposure above optimal temperatures accelerates development but increases mortality risk, particularly when combined with poor gravel conditions or flow disturbance. Temperature effects are therefore applied as conditional survival modifiers when incubation temperatures exceed biologically supported thresholds (Table 18). Note that the temperature range selected for the incubation life stage also sets the emergence timing as described in the next life stage transition (Beacham and Murray 1990; Asarian et al. 2023; Plumb et al. 2025), and incubation temperatures are adjustable by reach. Temperature selection will have some constraints to prevent cases that are not biologically correct. For example, model Reach 3 being cooler than model Reaches 1 and 2.

Temperature-development literature from outside the watershed supports the direction of this rule: warming accelerates development and increases metabolic and oxygen stress above favorable ranges. Table 18 multipliers are expert-derived values for discrete temperature bins.

Table 18. Incubation temperature categories and survival multipliers.

Incubation Temperature Condition	Indicative Mean Daily Temperature (°C)	Thermal Category	Biological Interpretation	Egg-to-Emergence Survival Multiplier
Optimal	≤10–12 °C	Optimal incubation	Near-optimal metabolic rates; high oxygen availability; low stress.	1.00
Cool–moderate	12–14 °C	Favorable	Slightly accelerated development; minimal stress. **Default.**	0.92
Warm-moderate	14–16 °C	Elevated	Increased metabolic demand; greater sensitivity to fines and low dissolved oxygen.	0.80
Warm	16–18 °C	Stressful	Sustained thermal stress; survival declines, especially in degraded gravel.	0.60
Very warm	>18 °C	High stress	High mortality risk; development may be rapid but inefficient.	0.40
Extreme	≥20 °C (sustained)	Failure zone	Metabolic failure; near-complete egg loss likely.	0.01

LFA Rules and Model Logic Overview

The following section provides an overview of the model logic (Steps) that feed into the LFA testing described in the next section. In this life stage, we start with redds and information on female spawners to estimate the number of eggs successfully deposited that survive through incubation to emergent fry. Survival through incubation is calculated as the product of redd construction success, female size-dependent egg quality, sediment effects, hydrologic disturbance, temperature stress, and thiamine status. This aggregation produces the emergent fry abundance that advances to juvenile rearing life stages, enabling clear attribution of early life-stage limitation to specific biological or habitat drivers.

STEP 1: Initialize Incubating Eggs by Female Age and Size

Inputs: Effective successful female spawners by age class and origin from previous life stage.

Calculation(s): Multiply successful female spawner abundance by age class and origin by fecundity in Table 12.

Table 12. Age-specific female size from Trinity River Hatchery returns and fecundity for Chinook salmon (Healey and Heard 1984).

Outputs: Total eggs deposited in the gravel by age class – note at this stage parentage by run-type or origin is no longer tracked in the model.

STEP 2: Female size × gravel size redd construction success

Inputs: Starting egg abundance by female parent age class from Step 1.

Calculation(s): Multiply total eggs by contributing female age class by female size and gravel size multipliers in Table 13.

Outputs: Total eggs retained in incubation after accounting for redd construction success.

STEP 3: Female size–dependent egg quality and fecundity modifier

Inputs: Incubating egg abundance by female parent age class from Step 2.

Calculation(s): Multiply total eggs by contributing female age class by female size and quality multipliers in Table 14.

Outputs: Total eggs after applying maternal egg quality survival.

STEP 4: Thiamine deficiency (maternal effect filter)

Inputs: Incubating egg abundance from Step 3.

Calculation(s): Multiply thiamine deficiency survival multipliers in Table 15.

Outputs: Total eggs surviving combined effects of all previous steps**.**

STEP 1-4 (Hatchery): Hatchery Origin Egg to Fry Survival

Inputs: Abundance of Hatchery origin spawners, separated by reach.

Calculation(s): Multiply total hatchery origin abundance by hatchery fecundity and survival multiplier to account for decreased hatchery reproductive success and egg-to-fry survival from maternal status, as well as thiamine deficiency survival multiplier and gravel size multipliers. When needed, age 3 is used as a proxy for hatchery origin fish.

Outputs: Total hatchery origin eggs surviving per reach based on maternal impacts on the eggs.

STEP 5: Spawning gravel quality (fine sediment) survival by reach

Inputs: Incubating egg abundance from Step 1 through 4.

Calculation(s): Multiply total eggs by fine sediment survival multipliers in Table 16.

Outputs: Total eggs surviving fine sediment effects.

STEP 6: Hydrologic disturbance during incubation (scour / dewatering) by reach

Inputs: Incubating egg abundance from Step 5.

Calculation(s): Multiply total eggs by hydrological survival multipliers in Table 17.

Outputs: Total eggs surviving hydrological disturbance effects.

STEP 7: Temperature-dependent incubation survival by reach

Inputs: Incubating egg abundance from Step 6.

Calculation(s): Multiply temperature survival multipliers in Table 18.

Outputs: Total eggs surviving combined effects of all previous steps to produce abundance of emergent fry.

Conceptual Basis for LFA Testing:

The following life-stage diagnostic tests evaluate whether limitations on early freshwater production arise during egg incubation and emergence, rather than from adult abundance, spawning capacity, or later juvenile processes. Because empirical information on spawning gravel size within Trinity River habitats is currently limited, gravel size is treated as a scenario-based conditioning variable rather than an observed driver. Accordingly, LFA tests focus on identifying threshold conditions and relative sensitivities under plausible gravel-size scenarios, rather than diagnosing observed reach-specific limitations. Tests are structured to isolate per-redd viability mechanisms—female size and age structure, gravel compatibility, fine sediment accumulation, hydrologic disturbance, incubation temperature, and maternal thiamine status—and to determine which factors act as primary versus compounding constraints on fry emergence. Similar to other LFA tests, we rely primarily on recovery targets to evaluate and classify limiting factors as a primary limiting factor (alone sufficient to explain the shortfall), a compounding limiting factor (important only in combination), or non-limiting (present but not constraining outcomes) with respect to adult Chinook salmon returns to the Trinity River.

Fall-run Chinook Salmon Targets:

1. Increase escapement of naturally produced fall-run Chinook salmon to 62,000.
2. Population supports harvest across all sectors of 131,750 adults.

Spring-run Chinook Salmon Targets:

1. Increase escapement of naturally produced spring-run Chinook salmon to 6,000.
2. Population supports harvest across all sectors of 12,750 adults.

Test 1: Is incubation survival the primary limiting factor on early freshwater production?

Hypothesis: Despite adequate spawner abundance and effective redd construction, losses during incubation and emergence impose a primary biological constraint on emergent fry production, such that poor incubation conditions alone can explain low early freshwater output and downstream limitations on adult escapement.

Approach: Apply baseline effective redd abundance and female age/size structure from the spawning life stage. Hold adult abundance, spawning capacity, and redd availability constant. Evaluate egg-to-emergence survival under two contrasting incubation scenarios:

- **Baseline incubation conditions**, reflecting current assumptions about gravel compatibility, fine sediment levels, hydrologic stability, temperature, and thiamine status.
- **Best-plausible incubation conditions**, defined by:
    - Gravel sizes compatible with most female size classes
    - Low fine sediment
    - Stable incubation flows
    - Favorable incubation temperatures
    - No thiamine deficiency

All downstream rearing, migration, and ocean survival processes are held constant to isolate the effect of incubation survival.

Under these conditions:

- Compare resulting adult escapement between baseline and best-plausible scenarios.
- Evaluate whether improving incubation survival alone can plausibly close the gap to adult recovery targets.

Diagnostics and Interpretation:

1. Large increase in adult escapement under best-plausible conditions → Incubation survival is a primary limiting factor on early freshwater production.
2. Minimal response in escapement → Incubation is not limiting; constraints occur later in the life cycle.

Management Interpretation:

This test determines whether Trinity-managed incubation conditions materially constrain population recovery. If incubation emerges as a primary bottleneck, habitat restoration and flow management during the incubation window represent viable recovery levers. If not, resources should be redirected toward later freshwater or marine life stages.

Test 2: Under what gravel-size conditions does female size become a dominant constraint on egg/embryo survival?

Hypothesis: Under plausible spawning gravel size distributions, mechanical constraints on redd construction disproportionately limit egg survival for smaller and younger females, such that emergent fry production becomes dependent on the largest females regardless of other incubation conditions.

Approach: Apply baseline female age and size structure and fecundity. Hold fine sediment, hydrologic stability, temperature, and thiamine status constant at favorable values. Evaluate a bounded set of spawning gravel size scenarios:

- Size-compatible gravel, allowing redd construction by most female size classes.
- Moderately coarse gravel, excluding younger/smaller females while permitting larger females to spawn successfully.
- Coarse gravel, permitting redd construction only by the largest females.

Under these conditions:

- Compare adult escapement across gravel scenarios.

Diagnostics and Interpretation:

1. Strong decline in adult escapement as gravel becomes coarser → Female size × gravel compatibility is a dominant bottleneck.
2. Moderate decline limited to scenarios excluding the smallest females → Gravel size acts as a compounding constraint.
3. Minimal response across gravel scenarios → Gravel size is unlikely to be a primary limiter under plausible conditions.

Management Interpretation:

This test evaluates whether substrate composition can impose a hard biological ceiling on productivity through demographic filtering. If gravel size is limiting, targeted gravel augmentation or recruitment actions may yield disproportionate benefits by restoring access to spawning habitat for a broader segment of the female population.

Test 3: Is chronic fine sediment the dominant bottleneck during incubation?

Hypothesis: Chronic fine sediment accumulation in spawning gravels imposes a primary constraint on egg-to-emergence survival, such that reductions in fine sediment alone would substantially increase emergent fry abundance and adult escapement across plausible gravel conditions.

Approach: Apply baseline female demographic structure and fecundity. Hold gravel size, hydrologic stability, temperature, and thiamine status constant. Evaluate a gradient of fine sediment scenarios across gravel conditions.

Under these conditions:

- Examine monotonic responses in escapement to increasing fines.
- Evaluate whether sediment operates independently or interacts strongly with gravel size.

Diagnostics and Interpretation:

1. Consistent, large declines in escapement with increasing fines → Fine sediment is a primary limiting factor.
2. Strong effects only under coarser gravel scenarios → Fine sediment is a compounding constraint.
3. Weak or inconsistent responses → Sediment is secondary relative to other incubation processes.

Management Interpretation:

This test determines whether watershed-scale sediment reduction efforts are likely to produce meaningful population-level benefits. A strong sediment signal supports prioritization of upslope restoration, road management, and sediment control actions.

Test 4: Do hydrologic disturbances during incubation materially reduce emergence success?

Hypothesis: Flow-driven disturbances during incubation (scour, burial, or dewatering) impose biologically meaningful losses that reduce emergent fry production and adult escapement, even under otherwise favorable habitat conditions.

Approach: Apply baseline female demographic structure and fecundity. Hold gravel size, fine sediment, temperature, and thiamine status constant. Evaluate a sequence of hydrologic disturbance scenarios ranging from stable conditions to severe disturbance.

Under these conditions:

- Compare adult escapement across disturbance levels.

Diagnostics and Interpretation:

1. Stepwise declines in escapement with increasing disturbance → Flow instability is a primary or compounding limiter.
2. Strong effects only under marginal gravel conditions → Hydrologic disturbance is conditional.
3. Minimal response → Hydrologic disturbance during incubation is not limiting.

Management Interpretation:

This test informs whether flow timing, ramping rates, and incubation-period protections can meaningfully improve early life-stage survival. If flow disturbance is limiting, management actions targeting incubation stability are warranted.

Test 5: Can maternal thiamine deficiency suppress emergence under favorable habitat conditions?

Hypothesis: Maternal thiamine deficiency imposes a biochemical constraint on egg survival that can limit emergence and adult escapement independent of freshwater habitat quality.

Approach: Under best-plausible habitat conditions (compatible gravel, low sediment, stable flows, favorable temperatures), evaluate no, mild, moderate, and severe thiamine deficiency scenarios. Run the same scenarios without ocean and in-river harvest impacts to remove harvest interaction effects.

Under these conditions:

- Compare emergent adult escapement across thiamine levels.

Diagnostics and Interpretation:

1. Large declines in escapement under deficiency → Thiamine deficiency is a primary or episodic limiter.
2. Moderate effects that interact with other stressors → Thiamine is a compounding factor.
3. Minimal response → Thiamine is not limiting under assumed ocean conditions.

Management Interpretation:

This test clarifies whether ocean-linked maternal effects cap freshwater productivity. If thiamine deficiency is limiting, habitat improvements alone may be insufficient to achieve recovery targets.

Test 6: Under best-plausible incubation conditions, where does the first early-stage bottleneck occur?

Hypothesis: Even when all controllable incubation constraints are relaxed, gains in egg-to-emergence survival may be insufficient to drive adult escapement toward recovery targets, indicating that limiting factors occur later in the life cycle.

Approach: Apply a best-plausible incubation scenario incorporating:

- Size-compatible gravel
- Low fine sediment
- Stable incubation flows
- Favorable temperatures
- No thiamine deficiency

Compare emergent fry abundance and downstream adult escapement to baseline outcomes and recovery targets.

Diagnostics and Interpretation:

1. Large fry and escapement increases approaching targets → Incubation is a major limiting stage.
2. Large fry gains with limited escapement response → Later life stages dominate limitation.
3. Fry increases insufficient to matter → Incubation is not a primary bottleneck.

Management Interpretation:

This test establishes whether alleviating incubation-stage constraints alone can realistically influence recovery trajectories. It provides a critical bridge between life-stage diagnosis and life-cycle relevance, guiding where restoration investments are most likely to produce population-level returns.

References

Alderdice, D. F. and F. P. J. Velsen. 1978. Relation between temperature and incubation time for eggs of Chinook salmon (Oncorhynchus tshawytscha). Journal of the Fisheries Research Board of Canada 35:69–75.

Asarian, J. E., K. De Juilio, S. Naman, D. Gaeuman, and T. Buxton. 2023. Synthesizing 87 years of scientific inquiry into Trinity River water temperatures. Riverbend Sciences.

Beacham, T. D., and C. B. Murray. 1990. Temperature, egg size, and development of embryos and alevins of five species of Pacific salmon: a comparative analysis. Transactions of the American Fisheries Society 119:927–945.

Beechie, T. J., H. Moir, and G. R. Pess. 2008. Hierarchical physical controls on salmonid spawning location and timing. American Fisheries Society Symposium 65:83–101.

Brown, S. B., J. D. Fitzsimons, J. C. Honeyfield, and D. E. Tillitt. 2005. Implications of thiamine deficiency in Great Lakes salmonines. Journal of Aquatic Animal Health 17:113–124.

Burner, C. J. 1951. Characteristics of spawning nests of Columbia River salmon. Fishery Bulletin of the Fish and Wildlife Service 61:93–100.

Buxton, T. H. 2021. History of fine sediment and its impacts on physical processes and biological populations in the restoration reach of the Trinity River, California. Report TRRP-2021-1 for the Trinity River Restoration Program. Trinity River Restoration Program.

DeVries, P. 1997. Riverine salmonid egg burial depths: review of published data and implications for scour studies. Canadian Journal of Fisheries and Aquatic Sciences 54:1685–1698.

Fisher, J. P., J. M. Spitsbergen, T. Iamonte, E. E. Little, and A. DeLonay. 1995. Pathological and behavioral manifestations of the "Cayuga syndrome," a thiamine deficiency in larval landlocked Atlantic salmon. Journal of Aquatic Animal Health 7:269–283.

Fitzsimons, J. D., B. Williston, G. Williston, L. R. Brown, A. H. El-Shaarawi, L. Vandenbyllaardt, J. C. Honeyfield, D. E. Tillitt, M. Wolgamood, and S. B. Brown. 2007. Egg thiamine status of Lake Ontario salmonines 1995–2004 with emphasis on lake trout. Journal of Great Lakes Research 33:93–103.

Gallinat, M. P., and W. Y. Chang. 2013. Phenotypic comparisons among natural-origin, hatchery-origin, and captive-reared female spring Chinook salmon from the Tucannon River, Washington. North American Journal of Aquaculture 75:572–581.

Healey, M. C., and W. R. Heard. 1984. Inter- and intra-population variation in the fecundity of Chinook salmon (Oncorhynchus tshawytscha) and its relevance to life history theory. Canadian Journal of Fisheries and Aquatic Sciences 41:476–483.

Heath, D. D., J. W. Heath, C. A. Bryden, R. M. Johnson, and C. W. Fox. 2003. Rapid evolution of egg size in captive salmon. Science 299:1738–1740.

Iritani, A. T., E. M. Barnes, and M. P. Phelps. 2025. Influence of egg size and parental genetics on the metabolic rate of Chinook and pink salmon embryos. Conservation Physiology 13:coaf062.

Kondolf, G. M., and M. G. Wolman. 1993. The sizes of salmonid spawning gravels. Water Resources Research 29:2275–2285.

Krause, A., P. Wilcock, and D. Gaeuman. 2010. One hundred and fifty years of sediment manipulation on the Trinity River, California. In Proceedings of the Joint Federal Interagency Conference on Sedimentation and Hydrologic Modeling. Las Vegas, Nevada.

Mantua, N. J., H. Bell, A. E. Todgham, M. E. Daniels, J. Rinchard, J. M. Ludwig, J. C. Field, S. T. Lindley, F. E. Rowland, C. A. Richter, and D. Walters. 2025. Widespread thiamine deficiency in California salmon linked to an anchovy-dominated marine prey base. Proceedings of the National Academy of Sciences 122(26):e2426011122.

Montgomery, D. R., J. M. Buffington, R. D. Smith, K. M. Schmidt, and G. R. Pess. 1996. Pool spacing in forest channels. Water Resources Research 31:1097–1105.

Montgomery, D. R., E. M. Beamer, G. R. Pess, and T. P. Quinn. 1999. Channel type and salmonid spawning distribution and abundance. Canadian Journal of Fisheries and Aquatic Sciences 56:377–387.

Ohlberger, J., D. E. Schindler, R. J. Brown, J. M. Harding, M. D. Adkison, A. R. Munro, L. Horstmann, and J. Spaeder. 2020. The reproductive value of large females: consequences of shifts in demographic structure for population reproductive potential in Chinook salmon. Canadian Journal of Fisheries and Aquatic Sciences 77:1292–1301.

Plumb, J. M., R. W. Perry, and K. De Juilio. 2025. Calibration of the Stream Salmonid Simulator (S3) model to estimate annual survival, movement, and food consumption by juvenile Chinook salmon in the restoration reach of the Trinity River, California, 2006–18. U.S. Geological Survey Open-File Report 2024-1070. https://doi.org/10.3133/ofr20241070

Reiser, D. W., and T. C. Bjornn. 1979. Influence of forest and rangeland management on anadromous fish habitat in the western United States and Canada: habitat requirements of anadromous salmonids. U.S. Forest Service, Pacific Northwest Forest and Range Experiment Station, General Technical Report PNW-96.

Tappel, P. D. and T. C. Bjornn. 1983. A new method of relating size of spawning gravel to salmonid embryo survival. North American Journal of Fisheries Management 3:123–135.

Wu, F. C. 2000. Modeling embryo survival affected by sediment deposition into salmonid spawning gravels: application to flushing flow prescriptions. Water Resources Research 36:1595–1603.

TRINITY RIVER REARING (EMERGENT FRY TO TRINITY RIVER OUTMIGRATION)

The Trinity River rearing module applies weekly survival, growth, habitat-capacity, and outmigration rules. Baseline weekly survival values are calibration anchors; temperature, food, disease, flow-mediated capacity, and size-dependent outmigration act as relative modifiers that shape abundance and size at Trinity River outmigration.

Description of Life Stage Transition:

This life stage represents the transition of juvenile Chinook salmon from Trinity River spawning gravel emergence through freshwater rearing and juvenile outmigration from the Trinity River mouth. During this period, juveniles grow, occupy available rearing habitats, redistribute downstream, and eventually emigrate from the Trinity River in response to biological requirements, environmental conditions, and habitat constraints. The outcome of this life stage is a time- and size-structured cohort of juveniles exiting the Trinity River, which forms the input to downstream freshwater, estuarine, and early marine life stages.

To maintain consistency with the escapement–spawning life stage, the Trinity River is divided into the same three model reaches. These reaches differ in geomorphic structure, rearing capacity, and thermal regimes, which influence juvenile growth opportunities, competition for habitat, and outmigration timing.

- **Reach 1:** (Lewiston Hatchery to Old Lewiston Bridge / Bucktail) — the upper 10.9 km below Lewiston Dam (hatchery-influence zone).
- **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).

Processes during this life stage are evaluated on a weekly timestep and expressed in relative time, rather than fixed calendar weeks. Weekly summaries of temperature, flow, food availability, and hatchery releases form a matrix that governs juvenile growth, rearing capacity constraints, and the timing and size at emigration. Emergence timing is anchored to the median emergence week, derived from incubation temperatures, and all subsequent weeks are indexed relative to that reference point. This approach preserves internal consistency across life stages and avoids imposing arbitrary spawning or calendar assumptions.

Key factors considered in this life stage include:

- Incubation temperature–driven emergence timing and spread
- Weekly water temperature by reach as a control on growth and migration cues
- Weekly food availability by reach as a control on growth rates
- Weekly Trinity River flow as a determinant of reach-specific rearing capacity
- Hatchery release timing and abundance as a temporary reduction in rearing capacity
- Size- and timing-dependent outmigration via temperature and capacity mechanisms

- Forced outmigration at a given size threshold

This life stage is explicitly bounded at the Trinity River mouth and does not include processes operating in the lower Klamath River, estuary, or ocean.

Assumptions for LFA and LCM Rules:

Emergence timing and temperature: Incubation temperature influences development rate and emergence timing, and emergence occurs across a window rather than in a single week (Alderdice and Velsen 1978; Beacham and Murray 1990; DeVries 1997; Asarian et al. 2023). The same reach-specific incubation temperature regime used to evaluate incubation survival (Table 18) is carried forward to determine the median emergence week for juvenile rearing (Table 19). Emergent fry abundance is then distributed across a five-week window centered on the median emergence week using temperature-dependent weekly emergence multipliers (Table 20). Warmer incubation temperatures shift emergence earlier and concentrate emergence near the center of the window, whereas cooler temperatures produce a broader, more symmetric emergence distribution. This approach keeps emergence timing internally consistent with incubation conditions and provides the weekly starting abundances used for growth, survival, and capacity calculations. Because directly transferable categorical emergence timing values for Table 19 bins were not identified, professional judgment was used to translate the continuous temperature–development relationship into discrete LFA timing categories consistent with Table 18.

Table 19. Temperature categories used in incubation survival and weekly emergence multipliers used to assign emergent fry by reach to weeks (-2, -1, 0, +1, +2). Ties to incubation temperature chosen from Table 18.

Incubation Temperature Condition (from Incubation Stage)	Thermal Interpretation	Week −2	Week −1	Week 0	Week +1	Week +2	Emergence Pattern Interpretation
Optimal (≤10–12 °C)	Slow, stable development	0.10	0.20	0.40	0.20	0.10	Broad, symmetric emergence around median
Favorable (12–14 °C)	Slightly faster development	0.10	0.20	0.40	0.20	0.10	Typical Trinity emergence distribution
Elevated (14–16 °C)	Accelerated development	0.15	0.25	0.35	0.15	0.10	Earlier-weighted emergence
Stressful (16–18 °C)	Rapid development under stress	0.10	0.20	0.40	0.20	0.10	Compressed but still heterogeneous emergence
High stress (>18 °C)	Very rapid and synchronized	0.05	0.15	0.60	0.15	0.05	Highly synchronized emergence
Failure zone (≥20 °C)	Truncated emergence	0.05	0.10	0.70	0.10	0.05	Narrow emergence window; many embryos lost

Table 20. Conceptual example of how the weeks of emergence would map to calendar weeks assuming typical peak emergence in March.

Relative Week	Approx. Calendar Timing
−2	late February
−1	early March
0	mid-March
+4	mid-April
+8	mid-May
+12	mid-June
+16	mid-July
+18	late July
+20	early August
+22	mid-August

Growth: Growth in the model is driven by a combination of temperature and food availability, which act as direct controls on growth, and indirectly through habitat capacity through its influence on rearing duration or access to rearing habitats. Observed growth rates of juvenile Ocean-type Chinook salmon in the Trinity River and comparable California systems span a wide continuum that is reflected in bimodal size distributions and migration pulses observed at rotary screw traps (RSTs; Apgar et al. 2020; Pinnix et al. 2022). RST monitoring consistently reveals two dominant juvenile outmigration groups: an early pulse of small fry or "non-natal rearing" migrants, and a later pulse of larger parr and pre-smolt "natal-rearing" migrants, with a relatively sharp transition between strategies occurring near 45 to 50 mm fork length (Apgar et al. 2020). The early group typically exhibits little in-river growth prior to emigration, consistent with low realized growth rates and rapid downstream movement shortly after emergence, while the later group remains in natal habitats for weeks to months and displays sustained positive growth trajectories before outmigration. Most natal-rearing juveniles captured at RSTs fall within intermediate size classes (~55 to 80 mm), while larger parr and smolt-size juveniles (>75 to 90 mm) are observed in years or habitats that provide sustained access to favorable temperature and food conditions (Healey 1991; Greene et al. 2005; Scheuerell et al. 2009; Apgar et al. 2020; Pinnix et al. 2022). A forced-emigration rule is applied at 100 mm fork length as a conservative model safeguard to prevent unrealistically long freshwater residence; this threshold is above the typical size range of natal-rearing juveniles observed in Trinity River RST data and is not intended to represent an empirical migration cue. Furthermore, research in the Trinity suggests that off-channel habitats can provide more appropriate water temperatures to enable more optimal growth when fish are able to access such habitats (Cooper-Hertel et al. 2022).

The model represents this empirically documented range of growth outcomes by anchoring growth to a single baseline growth rate of 0.30 mm/day (2.7 mm/week), which reflects moderate, biologically realistic rearing conditions for natal-rearing juveniles (Myrick and Cech 2001; Sommer et al. 2001; MacFarlane and Norton 2002; Myrick and Cech 2002; Marine and Cech 2004; Jeffres et al. 2008; Katz et al. 2017). The model then scales that baseline using weekly temperature and food multipliers (Table 21). Low realized growth occurs when juveniles experience cool temperatures, food limitation, or short residence times and aligns with the small fry and early migrant size classes observed at RSTs (Table 21). Moderate realized growth

corresponds to the dominant natal-rearing parr size distributions, while high realized growth reflects exceptional conditions associated with productive habitats and early access to downstream food subsidies (Table 21). Emergent fry are assumed to enter the rearing stage at an initial fork length of 35 mm, consistent with field observations of newly emerged Chinook salmon fry (Murray and McPhail 1988; Beacham and Murray 1990). From this starting size, cumulative weekly growth, mediated by temperature, food availability, and available residence time, allows us to simulate the size-structured migration patterns documented across years and populations, allowing the model to reproduce observed alternative juvenile migratory strategies without prescribing fixed size thresholds or migration types a priori. See Figure 1 for a conceptual graph showing growth trajectories under low, moderate, and high growth trajectories across weeks, which produces variation in size and timing of outmigration.

Table 21. Growth rate categories used to represent growth under a variety of conditions that are influenced by temperature, food availability, and access to productive habitats. RST = rotary screw trap.

Growth Category	Daily Growth Rate (mm/day)	Weekly Growth Rate (mm/week)	Typical Size Progression at RSTs	Interpretation Relative to RST Observations
Low growth	0.10–0.18	0.7–1.3	Fry to small parr (≈35–55 mm)	Consistent with early detections and late-season small migrants; often associated with food-limited mainstem conditions, cool early weeks, or prolonged residence under warming stress.
Moderate growth (baseline)	**0.30**	**2.4-2.9 (2.7)**	Parr to pre-smolt (≈55–75 mm)	Matches the dominant size classes observed during the core outmigration window at Pear Tree and Willow Creek RSTs in typical years.
High growth	0.45–0.60	3.2–4.2	Large parr to smolt-size juveniles (≈75–95+ mm)	Observed during productive years and periods of strong growth; associated with early access to food-rich habitats and optimal temperatures.

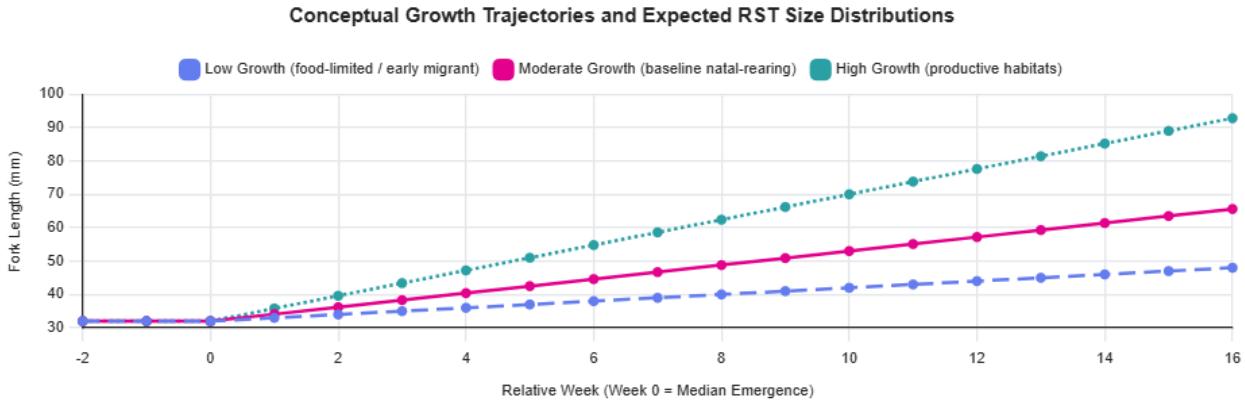

Figure 1. Conceptual illustration of how relative timing since emergence, realized growth trajectories, and residence duration can interact to simulate the size-structured juvenile Chinook salmon outmigration patterns observed at Trinity River rotary screw traps. Growth trajectories begin at an assumed emergence size of approximately 30 to 35 mm and diverge depending on temperature, food availability, and rearing

opportunity. Early migrants are dominated by small fry with minimal growth, while later migrants reflect sustained natal rearing and higher cumulative growth. The sharp transition near approximately 45 to 50 mm corresponds to the empirically observed shift between non-natal and natal-rearing migratory strategies. The late outmigration tail reflects residual movement under warm conditions, with size distributions determined by earlier growth history rather than continued growth.

Growth and temperature: Juvenile growth in the model is anchored to a baseline growth rate of 2.7 mm/week, which represents moderate natal-rearing conditions under favorable temperature and food availability conditions (Table 21). Temperature influences growth by modifying the baseline growth rate through weekly temperature-specific growth multipliers, reflecting well-established physiological constraints on metabolism and consumption (Table 22). Because directly transferable growth multipliers for the Table 22 temperature bins were not identified, the specific values were developed using professional judgment to translate the continuous temperature–growth relationship into model-ready relative growth scalars.

Growth potential is maximized within an optimal temperature range, where juveniles can fully express baseline growth, and declines progressively under cooler or warmer conditions. At low temperatures, growth is constrained by metabolic limitation, while at elevated temperatures the energetic benefits of continued rearing diminish rapidly as stress increases. These temperature-scaled growth rates are applied on a weekly basis to juveniles that remain rearing, allowing periods of rapid, moderate, or minimal growth to emerge from the thermal regime rather than being prescribed directly. This formulation ensures that cumulative growth, size-at-exit, and migration timing are mechanistically linked to seasonal temperature dynamics and are fully consistent with the temperature trajectories used to drive survival and outmigration in the model.

Simplified temperature trajectories that capture the dominant observed patterns were developed for the model to simulate interannual variation in Trinity River thermal conditions (Table 23). Each trajectory defines ranges of relative weeks over which temperature categories remain broadly stable, the resulting growth multiplier for each week is shown in Table 22. A cool/delayed warming trajectory maintains favorable rearing conditions for an extended period, promoting longer residence and delayed outmigration. A nominal/gradual warming trajectory reflects typical seasonal progression, with an early optimal growth window followed by a sustained transition into migration-favorable conditions. A rapid warming trajectory represents years when temperatures rise quickly after emergence, sharply reducing the duration of beneficial rearing conditions and compressing the rearing and outmigration periods. These trajectories are applied consistently across growth, survival, and migration processes, allowing differences in juvenile size distributions and migration timing to emerge from when warming occurs relative to emergence, rather than from arbitrary calendar dates. By summarizing temperature regimes in this way, the model remains consistent with a transparent and tractable structure to support the LFA.

Table 22. Baseline growth rates scaled by temperature category that can be used to drive weekly growth rates and simulate seasonal variations in temperature.

Temperature Category	Temperature Interpretation	Temperature Growth Multiplier (G_t)	Resulting Weekly Growth (mm/week)
<13 °C	Cold; metabolic limitation	0.60	1.6

Temperature Category	Temperature Interpretation	Temperature Growth Multiplier (G_t)	Resulting Weekly Growth (mm/week)
13–16 °C	Optimal rearing range	1.00	2.7
17–18 °C	Transitional; high but declining efficiency	0.90	2.4
18–20 °C	Warm stress emerging	0.70	1.9
>20 °C	Strong thermal stress	0.40	1.1

Table 23. Weekly trajectories of temperature that can be used to simulate different seasonal patterns of temperature in the Trinity River for each model reach. The default or baseline temperature trajectory is T2.

Trajectory Name	Relative Week Range	Dominant Temperature Category	Ecological Interpretation
Cool / Delayed warming (T1)	−2 to -1	<13–16 °C (Cold)	Prolonged cool conditions; strong rearing incentive; delayed migration
	+0 to +9	13–16 °C (Optimal)	Extended optimal growth window
	+10 to +12	17-19 °C (Transitional)	Gradual warming; migration pressure increases late
	+13 to +14	18–20 °C (Warm)	Late-season warming; residual migration tail, limited growth
	+15 to +22	>20 °C (Stress)	Thermal Stress; residual migration tail, limited growth
Nominal / Gradual warming (T2)	−2 to −1	<13–16 °C	Typical emergence under cool to optimal conditions
	0 to +9	13–16 °C	Extended optimal growth and rearing window
	+10 to +12	17–18 °C	Transitional warming; mixed rearing and migration
	+13 to +14	18–20 °C	Increasing thermal stress; sustained outmigration
	+15 to +22	>20 °C	Late-season warm conditions; migration favored, limited growth
Rapid warming / Early stress (T3)	−2 to +1	13–16 °C	Short optimal window post-emergence
	+2 to +4	17–18 °C → 18–20 °C	Rapid loss of growth benefit
	+5 to +22	>20 °C	Strong thermal stress; compressed migration window

Growth and food: Food availability influences juvenile growth by determining whether temperature-dependent growth potential can be fully realized, rather than by directly driving growth rates. In the model, growth is anchored to a single baseline rate representing moderate natal-rearing conditions, and food availability is applied as a multiplicative modifier to that baseline after temperature effects are accounted for. When food is sufficient, juveniles are assumed capable of meeting energetic demands associated with optimal temperatures, allowing full expression of temperature-scaled growth for each model reach (Table 24). When food is limited, realized growth is proportionally reduced even under otherwise favorable thermal conditions (Table 24). Food availability can be prescribed across relative weeks to represent changes in habitat connectivity, productivity, and restoration effectiveness, but it is not dynamically determined by the model. This simplified structure allows us to simulate the

influence of food availability without having to develop or integrate a complex bioenergetics submodule into the LCM. The simplified structure also reflects empirical evidence that prey availability is primarily controlled by access to productive habitats, such as floodplains, side channels, and low-velocity margins, rather than by temperature alone. By treating food as an independent, scenario-defined constraint on growth, the model preserves clear diagnostic separation between temperature-limited and food-limited growth, while allowing cumulative size outcomes and migration timing to emerge naturally from the sequencing and duration of favorable rearing conditions.

The model does not directly link habitat saturation to food availability. Habitat saturation is determined from the number and size of fish relative to available rearing habitat, whereas food availability is represented separately as a modifier of juvenile growth. Consequently, improved food conditions can increase growth and size at exit but do not increase modeled habitat capacity or prevent capacity-driven displacement. Modeling food limitation as density increases would require a more complex, dynamic relationship among fish density, prey production, consumption, and habitat conditions; that interaction is not included in this version of the model.

To represent variation in habitat productivity and prey availability without explicitly modeling prey populations (e.g., Healey 1991; Sommer et al. 2001; Jeffres et al. 2008), the model uses a small set of scenario-based food availability trajectories defined over relative time since emergence (similar to the example temperature trajectories presented previously in Table 25). Each trajectory specifies periods during which juveniles experience either food-sufficient or food-limited conditions, reflecting differences in access to productive habitats such as floodplains, side channels, and low-velocity margin habitats. Food availability is modeled as a modifier of growth potential rather than an independent driver of growth, scaling temperature-dependent growth according to whether juveniles can meet their energetic demands.

The frequency of food limitation is assumed to increase through the rearing period because energetic demands increase as juveniles grow, while prey abundance, prey size structure, and habitat-specific foraging opportunities may not increase proportionally. Studies have demonstrated that growth and survival of juvenile salmonids are strongly linked to food availability and net energetic gain, and that habitats incapable of providing sufficient food resources can create growth and survival bottlenecks. Kennedy et al. (2008) showed that food-limited juvenile salmon experienced reduced growth and survival when consumption rates fell below levels needed to maintain positive energy balance. Similarly, Dodrill et al. (2016) found that growth of larger salmonids can be constrained by both the abundance and size distribution of available prey, demonstrating that energetic demands increasingly depend on access to sufficiently large prey items. Together, these studies suggest that as juveniles increase in size, they become more susceptible to food limitation if prey resources do not scale with their energetic requirements.

Observed ontogenetic shifts in prey use by juvenile Chinook salmon further support this assumption. Merz and Vanicek (1996) and Merz (2001) found that juveniles consume larger and more energetically profitable prey as they grow, indicating increasing reliance on prey resources that may be less abundant or more spatially variable than smaller drift organisms. As a result, larger juveniles may require larger feeding territories, experience greater competition for prey

resources, and become increasingly sensitive to local habitat productivity. Under such conditions, growth may become density-dependent, and some individuals may redistribute or emigrate in search of more profitable foraging habitats, consistent with broader observations of movement responses among stream salmonids when energetic conditions deteriorate.

This conceptual framework is also supported by recent bioenergetic modeling of juvenile Chinook salmon. Luis et al. (2024) demonstrated that net energetic gain varies seasonally as fish size, macroinvertebrate abundance, temperature, discharge, and habitat conditions change through time. Their results suggest that growth opportunities are not constant over the rearing period and instead reflect temporal variation in habitat productivity and energetic profitability. Consequently, the model represents increasing likelihood of food limitation after approximately 5 weeks of rearing, not because age itself limits growth, but because larger juveniles are increasingly likely to encounter energetic constraints if habitat productivity does not keep pace with rising energetic demands.

Temporary food-sufficient periods represent early or sustained access to productive habitats that provide energetic subsidies, whereas food-limited periods represent rearing conditions dominated by less productive mainstem habitats. Food availability trajectories are prescribed by scenario and may vary among reaches and scenarios, allowing the model to evaluate whether the timing and duration of food subsidies are sufficient to influence cumulative growth, size at exit, and migration timing.

Food availability growth multipliers are based on the established bioenergetic principle that juvenile Chinook salmon growth depends on energy intake relative to metabolic demand. Published literature supports that prey availability, drift delivery, habitat complexity, and access to productive edge, side-channel, and floodplain habitats influence juvenile salmonid growth opportunity, while Trinity River S3 modeling provides system-specific support for representing food consumption as a mechanistic driver of growth in the restoration reach (Brett 1979; Myrick and Cech 2001; Plumb et al. 2025). Because directly transferable growth multipliers for the Table 24 food-availability categories were not identified, the specific values were developed using professional judgment to translate relative food conditions into model-ready growth scalars.

Table 24. Food availability categories and weekly growth multipliers that are applied weekly, along with temperature-based growth multipliers shown in Table 22.

Food Availability Category	Growth Modifier (G_f)	Interpretation
Food-limited	0.70	Rearing is dominated by mainstem habitats with limited prey density or quality; juveniles cannot fully meet energetic demand even under favorable temperatures
Food-sufficient	1.00	Access to productive habitats with abundant prey allows juveniles to fully express temperature-dependent growth potential

Table 25. Food availability trajectories designed to simulate natural variations in food availability.

Trajectory Name	Relative Week Range	Food Availability Category	Ecological Interpretation
Persistently food-limited (F1)	−2 to +22	Food-limited	Mainstem-dominated rearing with limited prey resources; little access to highly productive habitats
Early food pulse (F2)	−2 to −1	Food-limited	Limited productivity prior to emergence
	0 to +2	Food-sufficient	Short-term access to productive habitats immediately following emergence
	+3 to +22	Food-limited	Loss of connectivity; return to mainstem-limited conditions
Sustained early productivity (F3)	−2 to −1	Food-limited	Limited prey availability prior to widespread emergence
	0 to +4	Food-sufficient	Multi-week period of elevated prey availability supporting sustained early growth
	+5 to +22	Food-limited	Declining productivity as habitats disconnect and rearing shifts to mainstem
Optimized (F4, baseline)	−2 to −1	Food-limited	Pre-emergence conditions
	0 to +5	Food-sufficient	Well-timed connectivity of productive habitats aligned with peak growth window
	+6 to +22	Food-limited	Late-season mainstem rearing with reduced growth potential

Growth with temperature and food: Putting both temperature and food pieces together, we use the baseline growth rate and multiply both temperature and food multipliers by the baseline growth rate:

$$\text{Weekly Growth} = \text{Baseline Growth} \times G_t(\text{Temperature}) \times G_f(\text{Food})$$

This formulation ensures that growth emerges mechanistically from the interaction of thermal regime and habitat productivity, preserves diagnostic separation between temperature-limited and food-limited growth, and allows cumulative size trajectories and associated migration timing to reflect the sequencing and duration of favorable rearing conditions rather than prescribed size targets.

Survival: Weekly survival of juvenile Chinook salmon is represented as a background attrition process that is strongly influenced by water temperature and applied independently of growth and migration decisions. A single baseline weekly survival rate reflects low but persistent mortality under non-stressful conditions. Published studies have consistently demonstrated that juvenile salmonids experience continuous mortality during freshwater rearing as a result of predation, disease, environmental stress, competition, and movement processes, with mortality often increasing under thermally stressful conditions (Wedemeyer et al. 1980; Richter and Kolmes 2005; Mantua et al. 2010). Trinity River-specific modeling efforts similarly represent juvenile survival as a cumulative attrition process operating throughout freshwater residence and influenced by environmental conditions, particularly temperature. However, no study was identified that directly estimates a constant weekly rearing survival rate for Trinity River juvenile Chinook salmon. Consequently, baseline weekly survival (survival = 0.95/week) was treated as a calibration parameter selected to represent background mortality under non-stressful conditions

and to produce biologically realistic cumulative survival over observed freshwater residence periods.

Survival and temperature: Temperature modifies the baseline weekly survival through temperature-specific survival multipliers that capture increasing physiological stress, predation risk, and disease susceptibility as waters warm (Table 26). Survival remains near baseline under cool and optimal temperatures, declines modestly under transitional warming, and is progressively reduced under warmer conditions where stress and vulnerability intensify (Wedemeyer et al. 1980; Richter and Kolmes 2005; Mantua et al. 2010). These temperature-driven survival effects accumulate over time, contributing to the gradual thinning of juvenile cohorts, particularly during the late outmigration period. By linking survival directly to the same temperature trajectories used for growth and migration cues, the model ensures internal consistency while preserving diagnostic separation: temperature limits growth through energetic efficiency, influences migration through behavioral cues, and affects survival through cumulative stress. However, we note that survival at this life stage is not modeled as size-selective as it is in later life stages. In addition, predation is not directly modeled as a factor, but the weekly survival rate can be increased or decreased to simulate the effects of increased or reduced predation pressure. This formulation allows differences in abundance, size structure, and persistence to emerge naturally from the timing and duration of exposure to warm conditions, rather than from prespecified mortality events. Directly transferable weekly survival multipliers for the Trinity River temperature bins were not identified. Therefore, the specific multiplier values in Table 26 were developed using professional judgment to translate the literature-supported thermal stress gradient into model-ready weekly survival scalars.

Table 26. Temperature modifiers for weekly survival.

Temperature Category	Thermal Interpretation	Temperature Survival Multiplier (S_t)	Resulting Weekly Survival
<13 °C	Cool; low stress	1.00	0.95
13–16 °C	Optimal rearing	1.00	0.95
17–18 °C	Transitional; mild thermal stress	0.96	0.91
18–20 °C	Warm; moderate thermal stress	0.945	0.89
>20 °C	Stress; high thermal stress	0.92	0.87

Survival and Disease: Disease is represented in the model as a conditional modifier of weekly juvenile survival, acting in concert with temperature-mediated stress rather than as a constant or independent source of mortality (Table 27). Under cool or moderate thermal conditions, disease is assumed to play a negligible role in shaping survival (Ray et al. 2012; Bartholomew et al. 2022; Robinson et al. 2022), and baseline survival rates apply. As temperatures increase, residence time lengthens, flows decline, or crowding intensifies, disease risk can increase and contribute additional mortality beyond temperature effects alone (Ray et al. 2012; Bartholomew et al. 2022; Robinson et al. 2022). To capture this behavior without over-specification, disease effects are applied as scenario-based survival multipliers that scale weekly survival downward when disease pressure is elevated or high. Disease modifiers are not applied universally; instead, they are introduced only in selected scenarios designed to test whether disease could plausibly

act as a primary or compounding limiting factor, particularly during the late outmigration period when warm temperatures, low habitat capacity, and prolonged exposure are most likely. This approach allows the model to distinguish mortality arising from thermal stress alone from mortality that requires additional biological mechanisms, while preserving clear causal attribution within the LFA framework. Directly transferable weekly survival multipliers for the Table 27 disease categories were not identified. Therefore, the specific multiplier values were developed using professional judgment to translate the literature-supported disease-risk gradient into model-ready weekly survival scalars.

Table 27. Disease categories and survival modifiers.

Disease Pressure Category	Survival Modifier (S_d)	Interpretation
No disease pressure	1.00	Baseline condition; disease not contributing materially to mortality
Elevated disease risk	0.90	Moderate disease impacts under warm temperatures, crowding, or prolonged residence
High disease risk	0.80	Strong disease impacts during sustained warm, low-flow, high-stress conditions

Survival with temperature and disease: Weekly survival of juvenile Chinook salmon is modeled as a cumulative attrition process governed primarily by temperature and conditionally modified by disease pressure (Table 28). Temperature establishes the baseline level of physiological stress experienced by juveniles, with survival remaining near baseline under cool and optimal conditions, declining moderately under transitional warming, and falling further under sustained high temperatures. Disease does not act independently; instead, it is represented as a scenario-based modifier that compounds temperature-driven mortality when biologically plausible conditions—such as warm temperatures, low flows, crowding, or prolonged residence—are present. When disease pressure is absent, survival reflects temperature effects alone; when disease pressure is elevated or high, weekly survival is proportionally reduced across temperature categories, with the strongest combined effects occurring under warm conditions. Therefore, weekly survival is calculated as the product of a baseline survival rate, a temperature-dependent survival multiplier, and a disease modifier:

$$\text{Weekly Survival} = S_0 \times S_t(\text{Temperature}) \times S_d(\text{Disease})$$

Where:

- S_0 = baseline weekly survival (0.95),
- S_t = temperature survival multiplier (from Table 28),
- S_d = disease modifier (1.00, 0.90, or 0.80 depending on scenario).

This multiplicative formulation preserves clear diagnostic separation between thermal stress and disease processes, allows explicit "with versus without disease" comparisons in LFA, and ensures that cumulative mortality emerges from the timing, duration, and intensity of exposure rather than from prespecified mortality events.

Temperature trajectories define the primary physiological and ecological stress regime experienced by juvenile Chinook salmon, while disease pressure is introduced only in scenarios where conditions plausibly support infection and transmission (Table 29). Under cool or nominal

thermal regimes, disease is assumed to play a negligible role and survival is governed by background attrition and temperature effects alone. As temperatures warm rapidly and remain elevated, particularly when coupled with low flows, crowding, or prolonged residence, disease can act as a secondary stressor that compounds temperature-driven mortality. For this reason, disease trajectories are paired selectively with warm-stress temperature scenarios and applied as multiplicative survival modifiers rather than as independent mortality processes. This pairing structure allows LFA to distinguish outcomes driven purely by thermal stress from those that require additional biological mechanisms, while avoiding assumptions that disease is always present or uniformly important. By defining explicit temperature–disease scenario pairings, the model maintains causal clarity and supports transparent interpretation of survival limitation across contrasting Trinity River conditions.

Table 28. Combined survival multipliers with temperature and disease categories.

Temperature Category	Temperature Survival Multiplier (S_t)	No Disease (S_d = 1.00)	Elevated Disease (S_d = 0.90)	High Disease (S_d = 0.80)
<13 °C (Cold)	1.00	1.00	0.90	0.80
13–16 °C (Optimal)	1.00	1.00	0.90	0.80
17–18 °C (Transitional)	0.96	0.96	0.86	0.77
18–20 °C (Warm)	0.945	0.945	0.85	0.76
>20 °C (Stress)	0.92	0.92	0.83	0.74

Table 29. Examples of combining temperature and disease trajectories, with the assumption that temperature increases disease risk (prevalence) and survival effects. Temperature trajectories are based on those presented in Table 23.

Scenario Label	Temperature Trajectory	Disease Pressure	Conceptual Interpretation
Baseline	Nominal / Gradual warming (T2)	None	Typical Trinity River year; survival governed by temperature alone
Cool / Delayed warming	Cool / Delayed (T1)	None	Prolonged cool rearing with delayed warming; disease not expected to be a primary stressor
Warm stress	Rapid warming (T3)	None	Early and sustained thermal stress drives survival and migration; disease explicitly excluded
Warm + disease stress	Rapid warming (T3)	Elevated → High	Warm, low-flow, high-stress conditions where disease plausibly compounds thermal mortality
Optimized	Nominal / Cool (T1–T2)	None	Improved early conditions through restoration; disease not assumed despite higher fish residence
Diagnostic disease test	Nominal (T2)	Elevated	Stress test to isolate disease effects independent of extreme warming

Putting temperature, food, and disease together to generate weekly abundance by size class: To illustrate how temperature-driven emergence timing, temperature- and food-mediated growth, and temperature- and disease-mediated survival interact to shape juvenile size structure through time, we present a simplified, conceptual example (Table 30). The example assumes an initial abundance of 100,000 emergent fry and applies baseline growth under an optimal rearing temperature trajectory with food-sufficient conditions. This demonstration is intended solely to show how the model logic links sequential emergence, growth, and survival processes to produce weekly abundance by size class, prior to the application of rearing capacity limits and

outmigration rules. Values are illustrative and not prescriptive; all outcomes shown here are conceptual and subject to adjustment during model tuning and calibration as the full set of interacting processes is integrated.

Table 30. Example output showing growth of fry by week by length classes (in fork length [FL]) assuming baseline temperature, food, and disease trajectories. Values shown are conceptual and only intended to demonstrate model logic functionality.

Relative Week	FL <45 mm	FL 45–55 mm	FL 55–75 mm	FL >75 mm
-2	10,000	0	0	0
-1	29,700	0	0	0
0	68,809	0	0	0
1	86,745	0	0	0
2	85,289	8,853	0	0
3	65,025	26,293	0	0
4	27,662	60,916	0	0
5	9,127	76,794	0	0
6	0	75,506	7,837	0
7	0	57,566	23,277	0
8	0	55,839	22,579	0
9	0	23,755	52,311	0
10	0	7,837	65,946	0
11	0	0	71,570	0
12	0	0	69,423	0
13	0	0	67,340	0
14	0	0	65,320	0
15	0	0	63,360	0
16	0	0	61,460	0
17	0	0	59,616	0
18	0	0	57,827	0
19	0	0	56,092	0
20	0	0	49,293	5,117
21	0	0	47,814	4,963
22	0	0	46,380	4,814

Rearing, emigration, and flow: Juvenile outmigration in the model is governed by the interaction of flow-dependent rearing capacity, growth-mediated size structure, and limited background dispersal behavior, rather than by fixed migration dates or size thresholds (Table 31). At each weekly time step, juvenile abundance is tracked by size class and compared with rearing capacity for pre-smolt habitat, based on SRH-2D modeling and S3 relationships. S3 reports rearing habitat as the number of fry or parr that can be supported rather than as habitat area, which prevents a direct estimate of available rearing area. Because S3 capacity was also considered an overestimate by some TRRP members, available rearing capacity was established using expert-derived values during model tuning (Table 31). A small fraction of juveniles, particularly fry and, to a lesser extent, parr, are allowed to emigrate each week under a background, size-dependent migration propensity, representing early dispersal and non-natal

downstream movement observed in RST data (Table 32). Directly transferable weekly emigration probabilities for the Table 32 size classes were not identified. Therefore, the specific weekly values were developed using professional judgment to translate observed size-dependent dispersal patterns into model-ready background emigration scalars

Table 31. Rearing habitat capacity based on flow and reach.

Reach	Flow	Capacity (m2)
1	Low	300,000
1	Moderate	315,000
1	High	330,00
2	Low	315,000
2	Moderate	330,000
2	High	345,000
3	Low	330,000
3	Moderate	345,000
3	High	360,00

Table 32. Baseline outmigration propensity by size class applied weekly.

Size Class	Approx. Fork Length (mm)	Weekly Migration Propensity	Ecological Interpretation
Fry	<45 mm	3.5 % / week	Early dispersal and non-natal downstream movement common immediately following emergence
Small parr	45–55 mm	0.75 % / week	Limited exploratory movement; most individuals remain resident under favorable conditions
Parr / pre-smolt	55–75 mm	0.15 % / week	Rare voluntary outmigration prior to habitat or temperature forcing
Large parr / smolt-size	>75 mm	0 % / week	Outmigration primarily driven by capacity limitation or seasonal cues, not background dispersal

When total juvenile abundance exceeds available rearing capacity, capacity-forced migration occurs with larger fish getting habitat priority. Note that weekly capacity is determined by the weekly flow and the associated flow-dependent habitat area and capacity for that flow. Conceptually, at each weekly time-step (t), the number of juveniles forced to migrate based on capacity is determined as follows:

$$M_t^{\text{capacity}} = \max(0,\, N_t - K_t)$$

where:

- N_t= total juvenile abundance remaining in the reach at time t, after survival, growth, and background migration have been applied
- K_t= flow-dependent rearing capacity at time t, derived from hydraulically modeled habitat area and density assumptions
- M_t^{capacity}= number of juveniles forced to emigrate downstream during time step $t$due to habitat limitation

When $N_t \leq K_t$, no capacity-driven migration occurs.

Juvenile abundance N_t and capacity K_t are computed as the sum across size classes relevant to habitat availability:

$$N_t = \sum_i N_{i,t} \text{ and } K_t = \sum_i K_{i,t}$$

where i indexes size classes corresponding to rearing habitat.

The forced migrant total M_t^{capacity} is then based on size. Larger fish remain and rear while smaller fish are forced to emigrate.

The post-capacity abundance represents the remaining juvenile abundance in the reach after capacity forcing is defined as:

$$N_{t+1} = N_t\text{-}M_t^{capacity}$$

This ensures mass balance is preserved, abundance never exceeds capacity after forcing, and all displaced individuals are accounted for as outmigrants.

Temperature influences migration indirectly by modifying growth and survival and, later in the season, by reducing growth potential and favoring downstream movement under warm conditions. Together, these mechanisms produce realistic migration dynamics characterized by early fry dispersal, prolonged rearing when habitat conditions are favorable, and late-season outmigration driven primarily by habitat limitation and seasonal environmental stress.

Flow trajectories define seasonal patterns of Trinity River discharge that control rearing habitat availability, capacity persistence, and the feasibility of extended residence, including yearling strategies. Flow categories are translated into habitat area and capacity using SRH-2D relationships; they do not directly trigger migration or disease. Disease is linked to flow indirectly through warm temperatures, reduced habitat capacity, crowding, or prolonged residence, rather than as a separate direct flow–disease mechanism. Seasonal flow trajectories are represented as scenario-based weekly patterns that determine rearing habitat availability and capacity through time (Table 33; Plumb et al. 2025). Rather than prescribing discharge magnitudes, flow trajectories are defined in relative categories that are translated into habitat area using existing hydraulic relationships. This approach allows LFA to evaluate how the timing, duration, and persistence of flows—particularly spring recession and summer baseflow—control juvenile residence, size structure, and the potential emergence of yearling life-history strategies. Exact weekly flow trajectories and relative category assignments in Table 33 are scenario-based professional-judgment inputs developed to translate plausible seasonal hydrograph patterns into model-ready habitat-capacity trajectories.

Table 33. Flow-based rearing capacity trajectories that represent examples of seasonal flow regimes that can impact rearing capacity.

Trajectory ID	Scenario Name	Relative Week Range	Flow Category	Ecological Interpretation
FQ1	Persistently low flow (drought / stress year)	−2 to +6	Moderate	Typical winter/spring baseflow prior to emergence
		+7 to +10	Moderate → Low	Early recession; habitat contraction begins

Trajectory ID	Scenario Name	Relative Week Range	Flow Category	Ecological Interpretation
		+11 to +22	Low	Early capacity limitation; strong summer migration pressure
		+23 to +35	Low	Marginal summer rearing; limited holdover
		+36 to +55	Low	Poor overwinter refuge; low yearling potential
FQ2 (Baseline)	Nominal managed flow (baseline TRRP year)	−2 to +4	Moderate	Stable pre-emergence baseflow
		+5 to +9	High	Managed spring releases expand rearing habitat
		+10 to +16	Moderate	Gradual recession preserves rearing opportunity
		+17 to +22	Low	Late-season habitat contraction (end of model simulated rearing)
		+23 to +35	Low	Typical summer baseflow
		+36 to +55	Low → Moderate	Some overwinter habitat persists
FQ3	Extended spring high flow (restoration optimized)	-2 to +4	Moderate	Stable early baseflow
		+5 to +12	High	Extended spring habitat expansion
		+13 to +18	Moderate	Slow recession supports continued rearing
		+19 to +25	Moderate	Sustained summer rearing opportunity
		+26 to +35	Moderate → Low	Summer viability preserved
		+36 to +55	Moderate	Overwinter habitat sufficient for yearlings
FQ4	Flashy spring peak (short-duration high flow)	−2 to +3	Moderate	Typical baseflow
		+4 to +6	Very high	Short, intense spring peak
		+7 to +10	Moderate → Low	Rapid recession
		+11 to +22	Low	Post-peak habitat collapse
		+23 to +55	Low	Sustained summer–winter limitation
FQ5	High baseflow / yearling-favorable regime	−2 to +6	Moderate	Typical emergence conditions
		+7 to +15	High	Strong spring rearing opportunity

Trajectory ID	Scenario Name	Relative Week Range	Flow Category	Ecological Interpretation
		+16 to +25	Moderate	Sustained habitat into summer
		+26 to +35	Moderate	Summer holdover viable
		+36 to +45	Moderate	Overwinter refuge maintained
		+46 to +55	Moderate → High	Spring flow cue for yearling migration

Hatchery releases and capacity: Because hatchery-specific release dates, locations, fish size, and abundances were not provided, hatchery releases were represented using provisional relative-week scenarios spanning plausible early, baseline, and late release periods. These scenarios are intended for sensitivity testing of temporary habitat-occupancy effects and do not represent an observed Trinity River Hatchery release schedule. Hatchery releases are incorporated as time-specific additions to juvenile abundance and influence migration exclusively through their effects on rearing capacity. The model assumes a two-week residence time after release, based on the expectation that hatchery juveniles rapidly emigrate rather than permanently occupying Trinity rearing habitat (Balfour et al. 2025) and ensuring that hatchery releases do not permanently reduce available rearing habitat. When combined natural- and hatchery-origin abundance exceeds flow-dependent rearing capacity, capacity-forced migration occurs, requiring excess individuals to emigrate downstream, thereby inducing displacement of natural-origin juveniles through habitat limitation rather than behavioral interaction. This formulation allows hatchery influences on migration timing and magnitude to emerge mechanistically from habitat occupancy while preserving clear separation between natural growth- and habitat-driven processes. Hatchery fish are then removed from the rearing population after 2 weeks and are not counted as natural-origin production.

Yearlings: Empirical studies across the range of spring-run Chinook salmon indicate that expression of the yearling life-history strategy is highly variable and strongly dependent on habitat opportunity and environmental conditions, with no fixed proportion expected across systems or years (Beechie et al. 2006; Bourret et al. 2016; Schroeder et al. 2016). The analysis will not explore yearlings given that data on naturally produced yearlings are limited, but this life strategy has been added to the model when data becomes available. Yearlings are incorporated after growth and survival of Trinity rearing fish. For model simplicity, a portion of successful Trinity rearing juveniles will become yearlings and overwinter in the Trinity River. Yearlings will have an overwinter survival rate and then experience the same downriver conditions as Trinity rearing fish with higher survival rates due to being larger in size. This is a constant survival rate for the entire Trinity River emigration, not related to environmental conditions.

The default yearling proportion of 0.20 is a scenario/calibration parameter, not a Trinity River-specific estimate. California spring-run data support a smaller but important late-migrant/yearling pathway, while Pacific Northwest stream-type spring Chinook salmon can express much higher yearling emigration. Thus, 0.20 represents moderate expression of a recognized life-history strategy and should be tested through sensitivity analysis (Cordoleani et al. 2021; Healey 1991; Schroeder et al. 2016).

The yearling overwinter survival multiplier of 0.50 represents the assumed survival cost of remaining in freshwater through an additional winter before emigrating. Published Chinook salmon life-history literature supports the existence of both subyearling and yearling juvenile strategies and the tradeoff between longer freshwater residence, larger size at ocean entry, and additional freshwater mortality risk (Healey 1991; Greene et al. 2005; Scheuerell et al. 2009; Satterthwaite et al. 2014). Trinity River S3 modeling further supports representing juvenile survival, growth, movement, and food consumption as size- and season-dependent processes (Plumb et al. 2025). Therefore, 0.50 was selected using professional judgment as a coarse seasonal survival scalar for the yearling pathway and should be evaluated during calibration or sensitivity testing.

Yearling survival while emigrating through the Trinity River is set to 0.38 for the entire migration period due to yearling emigration not having a timing component. This survival value came from the Hoopa Tribal Fisheries JSATS survival study from 2022 to 2023.

Putting it all together: At each weekly time step, the model updates juvenile abundance sequentially to preserve mass balance and causal attribution. Juveniles first experience weekly mortality applied uniformly based on survival multipliers appropriate to temperature and disease conditions. Remaining juveniles grow according to baseline growth scaled by temperature and food availability and are reclassified into updated size classes. The fish are then subject to background migration, in which a small, size-dependent fraction emigrates regardless of habitat availability, representing early dispersal behavior. Hatchery releases, when present, are added and temporarily contribute to habitat occupancy. The model then evaluates flow-dependent rearing capacity; if total abundance exceeds capacity, capacity-driven forced migration is applied to remove all individuals in excess of available habitat, with larger fish obtaining rearing priority. Outmigrants produced through both background and capacity-driven processes are recorded by size class and exit timing bin corresponding to first-ocean-entry survival categories. The remaining juveniles progress to the next weekly time step, ensuring that abundance declines only through mortality or emigration and that all outmigrants are counted once and attributed to the week and size at exit.

Once juveniles reach a fork length of 100 mm they stop rearing behavior and emigrate out of the Trinity River. Published Chinook salmon life-history literature and Trinity River RST data support the distinction between early fry migrants, natal-rearing parr, and larger pre-smolt/smolt-size juveniles, with most natal-rearing juveniles observed in approximately the 55 to 80 mm range and larger juveniles generally exceeding 75 to 90 mm (Healey 1991; Greene et al. 2005; Scheuerell et al. 2009; Apgar et al. 2020; Pinnix et al. 2022). However, no directly transferable literature value was identified that requires emigration at exactly 100 mm. Therefore, 100 mm was selected using professional judgment as an upper-bound rearing size to prevent unrealistically long freshwater residence in the model.

We provide an example below using baseline assumptions and inputs to demonstrate how this model logic works and results in the abundance of outmigrants from the Trinity to the Klamath by size and timing bins (Table 34), which are then used in the next model step.

Table 34. Example simulation output using baseline conditions and an initial abundance of 100,000 fry and 30,000 fingerling fry (<55 mm) released over 3 weeks in weeks +4 to +6. This example is strictly to illustrate

model logic, not an actual simulation, and shows how emigrant production varies by size class and timing of entry into the Klamath River using the underlying model logic.

Timing Class	Fry <45 mm	Small Parr 45–55 mm	Parr / Pre-Smolt 55–75 mm	Large Parr >75 mm	Total Juvenile Outmigrants
Early (−2 to +4)	19,000	4,000	0	0	23,000
Core (+5 to +10)	8,000	21,000	15,000	0	44,000
Late (+11 to +16)	500	1,500	10,000	0	12,000
Very late (+17 to +22)	0	0	2,000	1,000	3,000
Total	**27,500**	**26,500**	**27,000**	**1,000**	**82,000**

Calibration limitations for juvenile outmigration size and timing: Willow Creek RST length data combine hatchery- and natural-origin fish, preventing separate estimation of natural-origin outmigrant sizes. Because the Trinity LCM tracks only natural-origin fish, the observed combined size distribution was not used to calibrate modeled emigration size. Juvenile outmigration timing was also not calibrated within the available project schedule. Willow Creek RST observations indicate that emigration generally occurs around mid-June, whereas baseline Trinity LCM outmigration occurs later. In the model, emigration occurs when fish become non-natal rearers, exceed 100 mm fork length, or encounter habitat limitations. Under baseline conditions, the latter two triggers occur infrequently, resulting in later emigration than observed. Consequently, modeled baseline outmigration timing should be viewed as an unresolved calibration limitation rather than a validated representation of observed outmigration timing.

Although the RST data were not used to calibrate outmigrant size or outmigration timing directly, the Willow Creek RST provides a useful empirical reference for average outmigrant size and outmigration timing in the Trinity River (Table 35). These data can therefore serve as a baseline for allocating outmigrants among emigration size and timing classes and for evaluating model performance during future calibration efforts.

Table 35. Monthly size (mm) at capture at Willow Creek rotary screw trap for subyearling (0+) and yearling (1+) (natural and hatchery origin combined), with range (minimum to maximum), 25th (Q25) and 75th (Q75) percentile, and mean length from trap years 2001-2024.

Life stage	Month	Min	Q25	Mean	Q75	Max
0+	Feb	45	45	45	45	45
0+	Mar	37	40	44	46	59
0+	Apr	38	44	52	60	76
0+	May	43	59	66	72	90
0+	Jun	61	76	82	87	95
0+	Jul	73	79	82	85	93
0+	Aug	75	83	86	89	105
0+	Sep	69	95	97	104	121
0+	Oct	104	137	136	140	150
0+	Nov	120	138	139	141	153
1+	Mar	86	99	104	108	150

Life stage	Month	Min	Q25	Mean	Q75	Max
1+	Apr	84	106	112	119	186
1+	May	82	111	117	116	219
1+	Jun	81	102	120	137	161
1+	Jul	100	102	105	104	124
1+	Aug	100	101	130	155	187

LFA Rules and Model Logic Overview

The following section provides an overview of the model logic (Steps) that feeds into the LFA testing described in the next section. Following these steps below, we arrive at the abundance of outmigrants produced in the Trinity River that enter the Klamath River by size- and timing-categories.

STEP 1: Initialize Emergent Fry (Temperature-Driven Emergence Timing)

Inputs: Abundance of emergent fry at the end of the incubation life stage for each reach after incubation survival multipliers are applied, and the temperature category experienced during incubation (note this specifically uses the temperature selected in the previous life stage so that there is internal consistency).

Calculation(s): The temperature category used in the incubation step (Table 18) is combined with Table 19 to distribute emergent fry across relative emergence weeks (e.g., Weeks −2 to +2, with Week 0 representing median emergence timing).

Outputs: Weekly abundance of emergent fry entering the juvenile rearing life stage in each reach.

STEP 2: Apply Weekly Survival

Inputs: Current weekly abundance of juveniles by reach and size class, weekly temperature category, and disease state (if applicable). See Table 28 for combined temperature and disease survival multipliers.

Calculation(s): Weekly survival is applied multiplicatively to all juveniles using baseline survival scaled by temperature- and disease-specific survival multipliers. Survival is applied uniformly across size classes within a reach.

Outputs: Post-survival juvenile abundance by reach and size class for the current weekly time step.

STEP 3: Apply Growth and Update Size Classes

Inputs: Post-survival juvenile abundance by reach and size class, baseline growth rate, weekly temperature category, and weekly food availability category. See Table 22 and Table 24 for temperature and food multipliers for growth.

Calculation(s): Weekly growth is calculated as the baseline growth rate scaled by temperature and food multipliers. Individual size is incremented accordingly, and juveniles are re-assigned to size classes based on fork length thresholds after the final growth step (e.g., fry, small parr, parr/pre-smolt).

Outputs: Updated juvenile abundance by reach and size class following growth.

STEP 4: Apply Background Migration Propensity

Inputs: Post-growth juvenile abundance by reach and size class, and background migration propensity rates by size class shown in Table 32.

Calculation(s): A small, size-dependent fraction of juveniles emigrate from each reach weekly based on background migration propensity values. Apply the migration propensity to each cohort based on size of the fish.

Outputs: Juvenile abundance by reach and size class after background migration is applied. Model track the number of juveniles that will move due to the migration propensity (juveniles move in step 8).

STEP 5: Add Hatchery Releases and Track Hatchery Residence

Inputs: Hatchery release schedule specifying release week(s) and abundance.

Calculation(s): Hatchery fish are added to juvenile abundance when evaluating habitat capacity, for two weeks after the release date. Hatchery fish are removed automatically after the two-week residence duration to represent rapid post-release emigration.

Outputs: Updated total juvenile abundance by reach, including both natural- and hatchery-origin fish contributing to habitat occupancy.

STEP 6: Calculate Flow-Dependent Rearing Capacity

Inputs: Weekly habitat–flow relationship-derived capacities for each reach for juvenile habitats.

Calculation(s): Flow is translated into available habitat area using flow-based habitat area and fish density multipliers. Habitat area is then converted into rearing capacity using fixed density assumptions. Total reach capacity is calculated as the sum of juvenile capacities.

Outputs: Weekly rearing capacity by reach.

STEP 7: Apply Capacity-Driven Forced Migration

Inputs: Total juvenile abundance remaining in each reach after background migration and hatchery additions, and total rearing capacity for each reach (Step 6).

Calculation(s): If total juvenile abundance exceeds rearing capacity, forced migration is calculated as the positive difference between abundance and capacity. All individuals in excess of capacity are required to emigrate downstream, with larger fish having preference, representing displacement due to habitat limitation.

$$M_t^{\text{capacity}} = \max(0, N_t - K_t)$$

Outputs: Number of capacity-forced migrants exiting each reach and juvenile abundance remaining after forced migration.

STEP 8: Advance Time Step and Track Migrants

Inputs: Post-migration juvenile abundance by reach, numbers of background- and capacity-driven migrants, and hatchery fish residence status.

Calculation(s): Migrants are transferred to the downstream reach or to the next life stage as appropriate. Juveniles remaining in the reach proceed to the next weekly time step. Hatchery residence counters are advanced, and hatchery fish exceeding their residence duration are removed.

Outputs: Weekly time-series of juvenile abundance by reach and size class, and cumulative migration by mechanism for diagnostic and LFA analysis.

STEP 9: Yearlings

Inputs: Total number of successful outmigrants by size class

Calculation(s): A user defined portion of total successful outmigrants will transition to the yearling pathway. The portion will be applied proportionally across the size groups.

Outputs: Yearlings that stay in the Trinity River to overwinter and abundance by size class of outmigrating juveniles.

Conceptual Basis for LFA Testing:

The LFA is designed to diagnose how environmental conditions and management actions interact with juvenile life-history processes to constrain or enhance freshwater production, migration timing, and size structure. Rather than attributing outcomes to single drivers in isolation, the LFA evaluates how growth opportunity, rearing capacity, and migration processes interact dynamically through time to shape juvenile abundance and size-at-exit.

In the model framework, juvenile production from the Trinity River emerges from four tightly coupled processes:

1. Temperature-driven emergence timing and growth determine when juveniles enter freshwater rearing and how rapidly individuals progress through size classes.
2. Flow-dependent rearing capacity, derived from habitat-flow relationships, limits how many juveniles can remain in each reach at any given time and links habitat to flow.
3. Background, size-dependent migration propensity allows early dispersal and non-natal movement to occur even when habitat is not limiting, producing realistic early fry migration.
4. Capacity-driven forced migration acts as a hard constraint when abundance exceeds rearing capacity, representing displacement due to habitat limitation and potential hatchery competition for space rather than behavioral choice.

Within this framework, migration is not prescribed by fixed size thresholds or dates but emerges from the interaction of growth, habitat availability, and seasonal context. Temperature modifies growth and the value of continued rearing rather than directly triggering migration, while flow governs habitat availability and therefore the capacity for juveniles to remain in rearing habitats. The LFA uses controlled combinations of temperature, flow, food availability, and hatchery release scenarios to isolate the mechanisms that most strongly limit freshwater production and size-structured outmigration.

To maintain interpretability and diagnostic power, the LFA focuses on a small set of core tests that span plausible Trinity River conditions and management levers. Each test is designed to diagnose whether a specific freshwater process limits the number, size, or timing of juvenile outmigrants in ways that could plausibly constrain adult escapement under reasonable downstream and marine survival assumptions. Tests alter only one or two processes at a time while holding all others constant, allowing clear attribution of outcomes to individual mechanisms.

Test 1: Is juvenile rearing habitat limiting under baseline Trinity River conditions?

Hypothesis: Juvenile freshwater production in the Trinity River is primarily constrained by flow-dependent rearing habitat capacity under baseline temperature, food, and hatchery release conditions. Under these conditions, juvenile abundance frequently exceeds available habitat before individuals can attain sizes associated with higher survival and recruitment. If rearing habitat is limiting, juveniles will be displaced early at small sizes, resulting in adult escapement projections below recovery targets even under favorable downstream survival.

Approach: Use baseline juvenile Trinity River rearing conditions, including temperature, flow, food availability, and hatchery releases. For each scenario, reduce rearing habitat by 10, 20, 25, 50, and 75%. Run these scenarios again without in-river and ocean harvest impacts. Evaluate juvenile dynamics weekly following modeled emergence, survival, growth, and background migration processes.

Track total juvenile abundance remaining in each reach and compare it directly to flow-derived rearing capacity at each weekly time step. When total abundance exceeds capacity, excess individuals are displaced via capacity-driven forced migration, independent of size or behavior.

This test explicitly evaluates habitat limitation after emergence and early survival processes have already been applied and holds temperature, food, growth, and survival assumptions constant to isolate the role of physical rearing capacity.

Baseline conditions include:

- Nominal temperature trajectory (T2)
- Baseline food availability (F4)
- Baseline flow regime (FQ2)
- Baseline hatchery release timing and magnitude
- Baseline growth and survival parameters

Under this structure:

- Incrementally evaluate weekly juvenile abundance relative to rearing capacity across the full rearing period.
- Track size structure and residence time of juveniles exiting the Trinity River under baseline conditions.

No density-dependent growth, behavioral habitat selection, or size-selective displacement is imposed; habitat limitation acts as a hard capacity constraint.

Diagnostics and Interpretation:

1. Frequent early capacity exceedance resulting in forced migration of fry and small parr → Juvenile rearing habitat capacity is limiting freshwater residence and constraining size at exit, resulting in smaller emigrating fish and low adult escapement.
2. Capacity exceedance occurring only at high juvenile abundance levels → Rearing habitat limitation is conditional and may only emerge under elevated production scenarios. This would lead to smaller juvenile outmigrants when juvenile abundance is high, resulting in lowered adult escapement.
3. Limited or delayed capacity exceedance with prolonged residence and larger outmigrants → Rearing habitat capacity is sufficient under baseline conditions; constraints must arise from other processes (e.g., temperature, food, survival, or downstream stages).
4. Strong temporal alignment between capacity exceedance and migration timing → Flow-dependent habitat availability is a primary control on juvenile migration dynamics.

These diagnosed size- and timing-structured juvenile outmigration patterns are then translated into expected adult escapement using standard downstream survival assumptions to evaluate whether baseline freshwater conditions are sufficient to meet escapement targets.

Management Interpretation:

This test determines whether current Trinity River flow regimes provide sufficient rearing habitat to support juvenile Chinook salmon throughout the freshwater rearing period under baseline environmental and hatchery conditions. If rearing habitat capacity is exceeded early and frequently, improvements in flow-dependent habitat availability (e.g., altered flow timing, increased habitat area, or extended spring flows) are required to increase juvenile residence time and size at exit. Under these conditions, rearing habitat quantity (flow or physical habitat) is identified as a primary escapement-limiting factor when juvenile outputs cannot meet escapement targets. If baseline rearing habitat limitation produces juvenile outputs that cannot meet escapement targets, rearing habitat quantity (flow or physical habitat) is identified as a primary escapement-limiting factor. Conversely, if rearing capacity is not limiting, management actions targeting temperature, food availability, hatchery interactions, or downstream survival are more likely to influence recovery outcomes.

Test 2: Do reasonable improvements in food availability alleviate rearing habitat limitation?

Hypothesis: If rearing habitat is limiting, increased food availability will increase residence time and size at exit but will not eliminate capacity-driven displacement or yield recovery-relevant escapement gains without additional habitat.

Approach: Run the model using baseline conditions, then apply the various food availability scenarios from Table 25. Hold temperature, flow regime, hatchery releases, growth formulation, and survival parameters constant. Evaluate adult escapement between the four scenarios.

This test explicitly evaluates whether increased productivity mitigates habitat limitation without altering physical habitat extent or flow-dependent capacity.

Under this structure, the logic chain is: Food improvement → growth/residence response → capacity interaction → migration response → escapement relevance

- Evaluate whether improved food delays the onset of capacity exceedance.
- Evaluate whether food-driven increases in size and residence time translate into a meaningful increase in projected adult escapement relative to baseline.

Diagnostics and Interpretation:

1. Minimal response to food enhancement → Constraints are structural (capacity or temperature), not energetic.
2. Larger response to food enhancement → Constraints have energetic interactions.

Management Interpretation:

This test determines whether productivity enhancement alone can meaningfully improve juvenile freshwater residence and size outcomes. If food improvements reduce displacement and increase size at exit, restoration actions targeting habitat productivity may be effective. If capacity limitation persists, increases in physical habitat or flow-mediated capacity will be required to achieve recovery gains. Food enhancement is considered escapement-relevant only if resulting juvenile outputs materially increase adult escapement toward recovery targets.

Test 3: Do reasonable temperature improvements alleviate juvenile limitation?

Hypothesis: Plausible improvements in temperature regime that extend the optimal growth window will increase juvenile growth rates and accelerate size progression but will not relieve rearing habitat limitation unless capacity constraints are reduced.

Approach: Apply an improved temperature trajectory representing extended or delayed warming (e.g., cool/nominal T1–T2 conditions) while maintaining baseline flow, food availability, hatchery releases, and survival structure. Evaluate juvenile outmigration size distribution and abundance as well as adult escapement.

This test isolates temperature as a growth-mediated mechanism operating within fixed habitat constraints.

Under this structure:

- Assess whether faster growth reduces time spent at high density relative to capacity.
- Evaluate shifts in size at exit and migration timing under improved temperature conditions.

Diagnostics and Interpretation:

1. Faster growth → Temperature improves growth but does not alleviate habitat limitation.
2. Increase in adult escapement → Temperature has impacts on adult escapement and may be a limiting factor.
3. Little change relative to baseline → Temperature is not a dominant limiting factor under current conditions.

Management Interpretation:

This test evaluates whether flow-managed temperature improvements alone can meaningfully improve juvenile freshwater performance. If improved temperatures increase size without reducing displacement, habitat or flow actions targeting capacity are required. If growth reduces crowding and displacement, temperature management may provide complementary benefits.

Test 4: Can the Trinity River produce sufficient juveniles under baseline conditions to meet recovery targets?

Hypothesis: Under baseline Trinity River conditions, juvenile freshwater processes alone do not produce sufficient abundance and size-structured outmigration to plausibly meet recovery targets when combined with reasonable ocean survival assumptions.

Approach: Use baseline rearing conditions and track juvenile outmigration by size and timing class and adult escapement. Increase Klamath River juvenile outmigration survival, ocean conditions, Klamath adult immigration survival, and Trinity adult immigration survival. With improved survivals, reduce rearing, spawning, and holding habitat simultaneously by 10, 25, and 50%.

Under this structure:

- Compare adult escapement across all scenarios.

Diagnostics and Interpretation:

1. Recovery targets not met even under favorable marine survival → Juvenile freshwater limitation is a primary bottleneck.
2. Targets met only with large late-season migrants → Extended residence and capacity are critical to recovery.
3. Targets met without freshwater modification → Constraints likely occur in downstream or marine stages.

Management Interpretation:

This test links freshwater limitation directly to recovery relevance. If baseline juvenile production is insufficient, targeted freshwater actions are required. The results help define the scale and type of improvements necessary to support recovery under realistic marine conditions.

Test 5: Do hatchery releases limit natural-origin juvenile production through rearing capacity interactions?

Hypothesis: Hatchery releases reduce natural-origin juvenile residence time and size at exit by temporarily occupying rearing habitat capacity and inducing displacement through capacity limitation.

Approach: Run the model with baseline conditions, run multiple scenarios with different release schedules ranging from no releases to 20 releases, as well as early and late release scenarios. Hatchery fish contribute to total abundance when evaluating capacity but are not credited as natural-origin migrants. This test evaluates hatchery effects exclusively through habitat occupancy rather than behavioral interference.

Under this structure:

- Compare capacity exceedance dynamics with and without hatchery releases.
- Evaluate changes in natural-origin size and timing distributions.
- Assess adult escapement.

Diagnostics and Interpretation:

1. Earlier migration and reduced large-parr production with hatchery releases → Hatchery occupancy limits natural-origin freshwater performance.
2. Minimal difference with and without hatchery releases → Capacity is sufficient to absorb hatchery pulses.
3. Strong sensitivity to release timing → Hatchery management may reduce displacement effects.

Management Interpretation:

This test determines whether hatchery practices constrain natural production through habitat competition. If hatchery effects are material, adjustments to release timing, size, or magnitude

may alleviate constraints without requiring habitat expansion. If effects are minimal, hatchery releases are unlikely to limit freshwater recovery efforts.

Test 6: Do Trinity River size and timing improvements propagate through downstream survival to adult returns?

Hypothesis: Improvements in Trinity River rearing flow conditions increase adult returns only if they produce more juveniles that leave the Trinity River at favorable sizes and timing, and those gains persist through lower Klamath River, estuary, and early marine survival.

Approach: Compare Trinity River rearing flow scenarios that produce different juvenile abundance, size, and outmigration timing profiles. Hold downstream lower Klamath River and estuary conditions constant for the primary contrast so that differences in ocean-entry survival and smolt-to-adult return reflect the Trinity-produced emigrant profile.

Under this structure:

- Evaluate whether early high-flow or low-capacity scenarios increase juvenile outmigration abundance but export fish at sizes that remain vulnerable during downstream transit.
- Evaluate whether scenarios that increase Trinity River residence time and growth produce larger juvenile outmigrants that survive better to ocean entry.
- Evaluate whether benefits to ocean entry persist through modeled smolt-to-adult return.

Diagnostics and Interpretation:

1. Larger or better-timed Trinity River juvenile outmigrants increase ocean-entry survival and smolt-to-adult return → Trinity River rearing conditions are a meaningful population-level limiting factor.
2. Trinity River outputs improve, but ocean-entry survival does not → Downstream Klamath River or estuary conditions filter out the upstream gains.
3. Ocean-entry survival improves, but smolt-to-adult return does not → Later life-stage or marine survival processes overwhelm juvenile-stage benefits.
4. Early-outmigration scenarios produce high abundance but low survival → Juvenile abundance alone is insufficient when fish leave the Trinity River too small or too early.

Management Interpretation:

This test links Trinity River juvenile production to life-cycle relevance. If improved rearing flow conditions increase both ocean-entry survival and smolt-to-adult return, management actions that expand rearing capacity, improve growth conditions, or better align flow timing with juvenile development should be prioritized. If gains are lost downstream, Trinity River actions must be paired with lower Klamath River, estuary, or broader life-cycle survival improvements to achieve recovery benefits.

References

Alderdice, D. F. and F. P. J. Velsen. 1978. Relation between temperature and incubation time for eggs of Chinook salmon (Oncorhynchus tshawytscha). Journal of the Fisheries Research Board of Canada 35:69–75.

Apgar, T. M., J. E. Merz, B. T. Martin, and E. P. Palkovacs. 2020. Alternative migratory strategies are widespread in subyearling Chinook salmon. Ecology of Freshwater Fish 30(1):125–139.

Asarian, J. E., K. De Juilio, S. Naman, D. Gaeuman, and T. Buxton. 2023. Synthesizing 87 years of scientific inquiry into Trinity River water temperatures. Report for the Trinity River Restoration Program (TRRP). Riverbend Sciences.

Balfour, T. J. B., D. J. A. Hurwitz, J. B. Atkinson, and E. Martins. 2025. Release strategies affect the freshwater residence and survival of hatchery-reared juvenile Chinook salmon. Transactions of the American Fisheries Society 154:278–290 https://doi.org/10.1093/tafafs/vnaf009.

Bartholomew, J. L., J. D. Alexander, S. L. Hallett, G. Alama-Bermejo, and S. D. Atkinson. 2022. Ceratonova shasta: a cnidarian parasite of annelids and salmonids. Parasitology 149:1862–1875.

Beacham, T. D. and C. B. Murray. 1990. Temperature, egg size, and development of embryos and alevins of five species of Pacific salmon: a comparative analysis. Transactions of the American Fisheries Society 119:927–945.

Beechie, T., E. Buhle, M. Ruckelshaus, A. Fullerton, and L. Holsinger. 2006. Hydrologic regime and the conservation of salmon life history diversity. Biological Conservation 130(4):560-572.

Bourret, S. L., C. C. Caudill, and M. L. Keefer. 2016. Diversity of juvenile Chinook salmon life history pathways. Reviews in Fish Biology and Fisheries 26(3):375-403.

Brett, J. R. 1979. Environmental factors and growth. Pages 599–675 *in* W. S. Hoar, D. J. Randall, and J. R. Brett, editors. Fish physiology, volume 8: bioenergetics and growth. Academic Press, New York. https://doi.org/10.1016/S1546-5098(08)60033-3

Cooper-Hertel, E. J., K. T. Lindke, T. Daley, K. De Juilio, and K. Hopkins. 2022. Assessing temperature regimes and juvenile Chinook Salmon growth in Trinity River off-channel and mainstem habitats. Report for the Trinity River Restoration Program (TRRP). Yurok Tribe Fisheries Department.

Cordoleani, F., C. C. Phillis, A. M. Sturrock, A. M. FitzGerald, A. Malkassian, G. E. Whitman, P. K. Weber, and R. C. Johnson. 2021. Threatened salmon rely on a rare life history strategy in a warming landscape. Nature Climate Change 11:982–988.

DeVries, P. 1997. Riverine salmonid egg burial depths: review of published data and implications for scour studies. Canadian Journal of Fisheries and Aquatic Sciences 54:1685–1698.

Dodrill, M. J., C. B. Yackulic, T. A. Kennedy, and J. W. Hayes. 2016. Prey size and availability limits maximum size of rainbow trout in a large tailwater: insights from a drift-foraging bioenergetics model. Canadian Journal of Fisheries and Aquatic Sciences 73(5):759-772.

Gowan, C. and K. D. Fausch. 2002. Why do foraging stream salmonids move during summer? Environmental Biology of Fishes 64(1-3):139-153.

Greene, C. M., D. W. Jensen, G. R. Pess, E. A. Steel, and B. E. Beamer. 2005. Effects of environmental conditions during stream, estuary, and ocean residency on Chinook salmon return rates. Transactions of the American Fisheries Society 134:1567–1592.

Healey, M. C. 1991. Life history of Chinook salmon (Oncorhynchus tshawytscha). Pages 311–394 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Jeffres, C. A., J. J. Opperman, and P. B. Moyle. 2008. Ephemeral floodplain habitats provide best growth conditions for juvenile Chinook salmon in a California river. Environmental Biology of Fishes 83:449–458.

Katz, J. V. E., C. A. Jeffres, J. L. Conrad, T. R. Sommer, J. Martinez, S. Brumbaugh, N. Corline, and P. B. Moyle. 2017. Floodplain farm fields provide novel rearing habitat for Chinook salmon. PLOS ONE 12:e0177409 https://doi.org/10.1371/journal.pone.0177409.

Kennedy, B. P., K. H. Nislow, and C. L. Folt. 2008. Habitat-mediated foraging limitations drive survival bottlenecks for juvenile salmon. Ecology 89(9):2529-2541.

Luis, S., R. Brown, K. Sellheim, and J. Merz. 2024. A spatially explicit drift foraging model quantifies salmon rearing habitat enhancement. Journal of Ecohydraulics 10(2):155-171.

MacFarlane, R. B. and E. C. Norton. 2002. Physiological ecology of juvenile Chinook salmon (Oncorhynchus tshawytscha) at the southern end of their distribution, the San Francisco Estuary and Gulf of the Farallones, California. Fishery Bulletin 100:244–257.

Mantua, N., I. Tohver, and A. Hamlet. 2010. Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. Climatic Change 102(1):187-223.

Merz, J. E. 2001. Diet of juvenile Chinook salmon in the lower Mokelumne River, California. California Fish and Game 87(3):102–114.

Merz, J. E. and C. D. Vanicek. 1996. Comparative feeding habits of juvenile Chinook salmon, steelhead, and Sacramento squawfish in the lower American River, California. California Fish and Game 82:149–159.

Myrick, C. A. and J. J. Cech. 2001. Temperature effects on Chinook salmon and steelhead: a review focusing on California's Central Valley populations. Bay-Delta Modeling Forum.

Myrick, C. A. and J. J. Cech Jr. 2002. Growth of American River fall-run Chinook salmon in California's Central Valley: temperature and ration effects. California Fish and Game 88:35–44.

Marine, K. R., and J. J. Cech Jr. 2004. Effects of high water temperature on growth, smoltification, and predator avoidance in juvenile Sacramento River Chinook salmon. North American Journal of Fisheries Management 24:198–210.

Murray, C.B. and J. D. McPhail. 1988. Effect of incubation temperature on the development of five species of Pacific salmon (Oncorhynchus) embryos and alevins. Canadian Journal of Zoology 66(1):266-273.

Pinnix, W. D., S. P. Boyle, T. Wallin, T. Daley, and N. A. Som. 2022. Long-term analyses of estimates of abundance of juvenile Chinook salmon on the Trinity River, 1989-2018. Arcata Fisheries Technical Series Report TS 2022-40. U.S. Fish and Wildlife Service.

Plumb, J. M., R. W. Perry, and K. De Juilio. 2024. Calibration of the Stream Salmonid Simulator (S3) model to estimate annual survival, movement, and food consumption by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in the Restoration Reach of the Trinity River, California, 2006–18 (No. 2024-1070). US Geological Survey.

Ray, R. A., R. A. Holt, and J. L. Bartholomew. 2012. Relationship between temperature and Ceratomyxa shasta–induced mortality in Klamath River salmonids. The Journal of Parasitology 98(3):520-526.

Richter, A. and S. A. Kolmes. 2005. Maximum temperature limits for Chinook, coho, and chum salmon, and steelhead trout in the Pacific Northwest. Reviews in Fisheries Science 13:23–49.

Robinson, H. E., J. D. Alexander, J. L. Bartholomew, S. L. Hallett, N. J. Hetrick, R. W. Perry, and N. A. Som. 2022. Using a mechanistic framework to model the density of an aquatic parasite, Ceratonova shasta. PeerJ 10:e13183.

Satterthwaite, W.H., Mohr, M.S., O'Farrell, M.R., Anderson, E.C., Banks, M.A., Bates, S.J., Bellinger, M.R., Borgerson, L.A., Crandall, E.D., Garza, J.C., Kormos, B.J., Lawson, P.W. and Palmer-Zwahlen, M.L., 2014. Use of genetic stock identification data for comparison of the ocean spatial distribution, size at age, and fishery exposure of an untagged stock and its indicator: California Coastal versus Klamath River Chinook salmon. Transactions of the American Fisheries Society, 143(1), pp.117-133.

Scheuerell, M. D., R. W. Zabel, and B. P. Sandford. 2009. Relating juvenile migration timing and survival to adulthood in two species of threatened Pacific salmon (Oncorhynchus spp.). Journal of Applied Ecology 46(5):983-990.

Schroeder, R. K., L. D. Whitman, B. Cannon, and P. Olmsted. 2016. Juvenile life-history diversity and population stability of spring Chinook salmon in the Willamette River basin, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 73(6):921-934.

Sommer, T. R., M. L. Nobriga, W. C. Harrell, W. Batham, and W. J. Kimmerer. 2001. Floodplain rearing of juvenile Chinook salmon: evidence of enhanced growth and survival. Canadian Journal of Fisheries and Aquatic Sciences 58:325–333.

Ward, D. M., K. H. Nislow, and C. L. Folt. 2009. Increased population density and suppressed prey biomass: relative impacts on juvenile Atlantic salmon growth. Transactions of the American Fisheries Society 138(1):135-143

Wedemeyer, G. A., R. L. Saunders, and W. C. Clarke. 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. Marine Fisheries Review 42:1–14.

KLAMATH RIVER JUVENILE OUTMIGRATION

Description of Life Stage Transition:

This life stage represents the transition of juvenile Chinook salmon from Trinity River juvenile outmigration through the lower Klamath River and estuary to ocean entry. As described by Apgar et al. (2020), fall Chinook salmon typically follow one of two rearing strategies prior to this transition: natal-rearing juveniles that remain in their natal stream, attain relatively large size, and migrate rapidly to the estuary, and non-natal-rearing juveniles that emigrate shortly after emergence and rear in downstream river habitats or tributaries before entering the estuary. These alternative pathways establish size- and timing-dependent differences prior to Klamath River entry. Accordingly, conditions encountered during Klamath River and estuary outmigration primarily act to select among pre-formed juveniles, such that this life stage is conceptualized as a survival and filtering process rather than a locus of substantial growth or production.

During juvenile outmigration through the Klamath River and estuary, survival is influenced by water temperature, disease exposure, flow conditions, travel time, access to thermal refugia, and timing of migration relative to seasonal warming (Ray et al. 2012; Plumb et al. 2019; Plumb et al. 2023). Emigration duration and growth during this stage are generally assumed to be negligible relative to upstream rearing stages; instead, size and timing inherited from Trinity emigration strongly condition exposure duration, physiological stress, and infection risk (Plumb et al. 2019; Plumb et al. 2023). However, we include an estuary growth pathway for smaller and earlier emigrants to represent the potential benefits of increased growth opportunity for estuary rearing (MacFarlane and Norton 2002). The outcome of this life stage is a size- and timing-structured cohort of juveniles successfully entering the ocean, which forms the input to the first-ocean-year survival and ocean maturation stages.

The Trinity River Restoration Program reports indicate that juvenile Chinook salmon survival in the lower Klamath River during juvenile outmigration mortality can be substantial and highly variable, particularly under warm temperature regimes (e.g., Pickard et al. 2023). Survival through this corridor is expected to follow strong nonlinear responses to water temperature, with marked declines observed as temperatures exceed approximately 18 to 20 °C, often in conjunction with elevated disease pressure and prolonged exposure (Ray et al. 2012; Plumb et al. 2019; Plumb et al. 2023).

This life stage is therefore conceptualized as a context-dependent survival filter, where upstream improvements in juvenile size and migration timing may or may not translate into increased ocean entry depending on downstream conditions. The modeling framework emphasizes scenario-based representation of stress regimes, allowing LFA to evaluate whether this stage constitutes a dominant bottleneck under baseline conditions and whether improvements in upstream production meaningfully propagate through to ocean entry.

Key factors considered in this life stage include:

- Size and timing of entry into the Klamath River
- Temperature and disease-driven survival based on flow conditions

Assumptions for LFA and LCM Rules:

The LFA assumptions and LCM rules presented here are subject to revision during final calibration and tuning. Processes and exact values may change. This documentation will be updated to reflect the finalized model.

Klamath River Juvenile Outmigration: Juvenile outmigrants through the lower Klamath River and estuary migration corridor are assumed to experience little to no meaningful growth prior to ocean entry (Plumb et al. 2023), such that fork length and size class at this stage are determined almost entirely by rearing in the Trinity River. Migration through the lower Klamath for Trinity-origin juveniles is assumed to be rapid relative to the duration of natal freshwater rearing and is dominated by exposure to thermal stress, disease risk, and travel time rather than by access to productive feeding habitats (Plumb et al. 2023). With these assumptions, we also do not consider capacity processes during Klamath River outmigration (Plumb et al. 2019; Plumb et al. 2023). Consequently, this life stage is modeled as a survival- and selection-dominated transition rather than a growth phase. Juveniles therefore enter the Klamath River carrying their size history inherited from Trinity River rearing, and that size is propagated unchanged through Klamath emigration and into ocean entry. Larger juveniles are assumed to experience improved survival not because of continued downstream growth, but because increased size confers reduced exposure duration, greater physiological tolerance, and lower relative susceptibility to disease and acute stressors (Zabel and Anderson 1997; Richter and Kolmes 2005; Ray et al. 2012). This formulation preserves a clear separation between upstream formation processes and downstream selection processes, allowing LFA to evaluate whether improvements in Trinity River growth and timing translate into meaningful gains at ocean entry or are subsequently filtered by downstream environmental conditions.

Temperature, disease, and survival: Juvenile survival through the lower Klamath River and estuary migration corridor is governed by the combined effects of water temperature, disease pressure, and exposure duration, all of which vary systematically with outmigration timing. Temperature establishes the primary physiological stress regime experienced by emigrants: survival is generally high under cool to moderate temperatures but declines rapidly as temperatures approach and exceed approximately 18 to 20 °C, where metabolic stress, reduced immune function, and pathogen virulence intensify (Table 36). Disease, particularly *Ceratonova shasta*–associated mortality, acts as a conditional secondary stressor, compounding temperature-driven mortality under warm, low-flow conditions and prolonged exposure (Wedemeyer et al. 1980; Richter and Kolmes 2005; Mantua et al. 2010; Ray et al. 2012). The literature supports the direction of the response that greater mortality occurs under elevated or high disease pressure, with smaller juveniles assigned greater vulnerability due to longer exposure and lower physiological buffering. However, directly transferable survival multipliers for the exact disease categories and size classes were not identified. Therefore, the numeric values were developed using professional judgment to translate the literature-supported disease-risk gradient into model-ready LFA survival scalars (Table 37).

Migration timing and travel duration determine how long juveniles are exposed to these stressors; earlier emigrants typically experience longer residence and exposure within the lower Klamath River because they arrive before completing smoltification, resulting in extended use of

downstream habitats. However, they generally encounter cooler temperatures and lower disease pressure. In contrast, later-timed migrants are more fully smoltified and transit the system more rapidly, reducing exposure duration, but they enter the lower river later in the season when temperatures and disease risk are often higher. Published work supports treating lower Klamath emigration as a survival- and selection-dominated stage with limited growth, where size and timing inherited from Trinity River rearing affect downstream exposure and vulnerability (Zabel and Anderson 1997; Richter and Kolmes 2005; Ray et al. 2012; Plumb et al. 2019; Plumb et al. 2023). The literature supports the direction of the response (Table 38), but directly transferable survival multipliers for the exact timing and size classes were not identified. Therefore, the numeric values were developed using professional judgment to represent relative exposure-duration risk across migration timing and size classes.

Importantly, temperature does not directly control migration in this stage but instead determines whether exposure during migration is benign or severe. Together, these processes create a nonlinear survival filter in which relatively small differences in temperature regime or migration timing can lead to large differences in survival, allowing downstream conditions to strongly mediate whether improvements in upstream juvenile size and timing ultimately translate into increased ocean entry.

Survival through the lower Klamath River and estuary migration corridor is calculated as a multiplicative combination of three components:

$$\text{Survival}_{\text{total}} = S_T \times S_E \times S_D$$

Where:

S_T= Temperature-regime survival multiplier (Table 36), applied equally across size classes

S_E= Exposure duration (migration timing / travel time) multiplier (Table 38)

S_D= Disease presence / exposure multiplier (Table 37)

Size class influences exposure effects and disease sensitivity, not temperature directly. Klamath River flow scenarios determine the associated temperature and disease categories because flow affects water temperature, migration duration, and pathogen exposure. Literature supports these mechanisms, but the categorical survival multipliers, including the nominal temperature multiplier of 0.82, are expert-derived values used for calibration and sensitivity analysis rather than empirical estimates of absolute survival.

Table 36. Temperature categories used to inform survival during Klamath River outmigration.

Temperature Regime	Approx. Condition	Survival Multiplier S_T	Interpretation
Cool	<15–16 °C	**0.97**	Minimal thermal stress; high physiological tolerance
Nominal	16–18 °C	**0.82**	Moderate stress; survival still relatively high
Warm	18–20 °C	**0.52**	Strong stress; rapid survival decline
Hot / Extreme	>20 °C	**0.2**	Acute stress; high mortality likely

Table 37. Disease presence and exposure multipliers used during Klamath River outmigration. This multiplier represents additional mortality associated with disease exposure (e.g., *Ceratonova shasta*, columnaris-type infections) during lower Klamath River and estuary migration. Disease effects are

conditional on temperature and exposure, and therefore compound temperature and timing effects rather than replacing them.

Disease Pressure Category	Fry <45 mm	Small Parr 45–55 mm	Parr / Pre-Smolt 55–75 mm	Large Parr / Smolt >75 mm	Ecological Interpretation
None	**1.00**	**1.00**	**1.00**	**1.00**	No disease contribution to mortality
Elevated	**0.68**	**0.73**	**0.78**	**0.88**	Moderate infection risk under warm, moderate-exposure conditions
High	**0.40**	**0.53**	**0.63**	**0.75**	Strong disease-mediated mortality during sustained warm, high-exposure conditions

Table 38. Exposure and migration duration survival multipliers used during Klamath River outmigration. Very Late migrants experience shorter exposure duration but may encounter warmer absolute temperatures; temperature and disease multipliers still apply independently and are linked to flow conditions.

Timing Class	Exposure Interpretation	Fry <45 mm	Small Parr 45–55 mm	Parr / Pre-Smolt 55–75 mm	Large Parr / Smolt >75 mm
Early (−2 to +4)	Long exposure, slow transit	0.30	0.40	0.45	0.50
Core (+5 to +10)	Moderate exposure	0.40	0.55	0.60	0.70
Late (+11 to +16)	Reduced exposure	0.55	0.65	0.90	0.96
Very late (+17 to +22)	Shortest exposure	0.45	0.60	0.80	0.75

River flows and migration: Trinity River and Klamath River flows influence juvenile survival during juvenile outmigration indirectly by modifying thermal conditions and disease risk, and access to refugia rather than by acting as independent survival drivers (e.g., Beechie et al. 2006; Plumb et al. 2019). Higher Klamath River flows reduce travel time and cumulative exposure, improving survival by increasing effective exposure multipliers, while lower flows extend residence and intensify exposure-related mortality, particularly under warm conditions (Zabel and Anderson 1997; Plumb et al. 2019; Plumb et al. 2023). Trinity River inflows can locally mitigate downstream thermal and disease stress through cooling and dilution effects, but only when discharge and temperature conditions align with migration timing. In the model, these flow effects are represented through scenario-based assignment of temperature and disease multipliers (Table 39), allowing LFA to evaluate whether downstream survival is constrained primarily by flow-mediated thermal stress, disease, or their interaction (e.g., Ray et al. 2012; Plumb et al. 2019).

Table 39. This table defines integrated flow scenarios that link Trinity River and Klamath River discharge to the temperature and disease multipliers applied during juvenile outmigration. Flow affects survival only indirectly, by shaping these multipliers – please see Table 36 and Table 37 for associated multipliers for each scenario.

Flow Scenario	Klamath Flow Condition (S_T)	Trinity Flow Condition	Temperature Regime (ST)	Disease Pressure (SD)	Conceptual Interpretation
High flow (cool)	Cool	High, cool Trinity inflows	Cool (high ST)	None (high SD)	Fast migration, minimal thermal and disease stress; downstream survival high for all size classes
Nominal flow (typical year, baseline)	Nominal	Moderate Trinity inflows	Nominal (moderate ST)	Elevated (moderate SD)	Typical Trinity–Klamath year; survival depends on size and timing
Low flow (warm, stressed)	Warm	Low or warm Trinity inflows	Warm (low ST)	High (low SD)	Prolonged exposure, strong thermal and disease-mediated mortality
Low flow (Trinity cooling)	Nominal	High, cool Trinity inflows	Nominal (moderate ST)	Elevated (moderate SD)	Trinity dilution provides partial thermal and disease relief but does not reduce exposure duration
Extreme stress	Hot/Extreme	Low, warm Trinity inflows	Hot / Extreme (very low ST)	High (low SD)	Severe mortality across most sizes and timings; downstream bottleneck dominates
Restoration-optimized	Cool	High, cool Trinity inflows	Cool (high ST)	None (high SD)	Idealized but plausible management outcome; strong propagation of Trinity production benefits

Estuary rearing: Although growth during lower Klamath River juvenile outmigration is generally assumed to be negligible for most juveniles, empirical studies demonstrate that limited estuarine rearing can provide a growth opportunity for a subset of early-timed, small fry migrants that enter the Klamath River estuary prior to the onset of physiologically stressful summer conditions (Wallace and Collins 1997; MacFarlane and Norton 2002; Beamer et al. 2005). Observations from the Klamath River estuary indicate that interannual variation in river flow and upstream rearing conditions strongly influences the extent of estuarine use: in high-flow years, most juvenile Chinook salmon reached the estuary at sizes sufficient for rapid migration to the ocean, whereas in low-flow years, smaller juveniles may be more likely to remain in the estuary for short-duration rearing prior to ocean entry (Wallace and Collins 1997).

Empirical observations and synthesis analyses further suggest that fry entering the estuary early in the season may encounter relatively cool water temperatures, elevated prey availability, persistent freshwater surface layers, and reduced disease pressure, permitting modest but biologically meaningful growth over brief residence periods (Healey 1980; Wallace and Collins 1997; Moore et al. 2016). In contrast, juveniles arriving later in the season, or under warm, low-flow estuarine conditions, are unlikely to benefit from estuarine growth and instead experience the estuary primarily as a migratory corridor with limited rearing opportunity.

In the model, estuarine growth is therefore represented as an optional, scenario-based process, applied only to fry-size juveniles (< 45 mm) migrating during early timing windows under favorable thermal and flow conditions. Under these circumstances, estuarine residence is assumed to result in limited growth sufficient for some individuals to transition into larger size classes (e.g., small parr) prior to ocean entry, potentially improving early marine survival. This growth pathway is assumed to be strongly timing-limited, context-dependent, and non-persistent across years, allowing the model to evaluate whether early estuarine connectivity can convert downstream dispersal into productive rearing for a small fraction of juveniles without assuming widespread or consistent estuarine production (Wallace and Collins 1997).

To represent this possibility without imposing explicit estuarine habitat capacity constraints, estuarine growth is implemented as a conditional process (Table 40), intended primarily to support the LFA until additional empirical data become available describing Trinity River Chinook salmon use of the Klamath River estuary.

Table 40. Size- and timing-based filters used to move fry to next size class prior to ocean entry to simulate potential estuary rearing and growth benefits.

Condition Category	Growth Applied	Resulting Size Transition	Interpretation
Baseline (no estuary growth)	None	Fry remain <45 mm	Estuary functions only as migration corridor
Limited estuary benefit	+10mm FL	Fry → Small parr (45–55 mm)	Small subset converts dispersal into productive rearing
Moderate estuary benefit	+15 mm FL	Fry → Small parr or lower parr	Strong estuary access in productive years
Upper-bound test (LFA Only)	+20 mm FL	Fry → Parr (55–75 mm)	Diagnostic "best plausible" scenario

Yearlings: Yearlings will also outmigrate through the lower Klamath River and the estuary without the benefit of rearing. After overwintering, yearlings will outmigrate from the Trinity River to the estuary with different survivals for the lower Klamath River and the estuary (Table 41). In the Klamath River, we assume survival is ~ 92% based on 2022 to 2023 JSATS survival study data provided by the IDT (Hoopa Tribe). During estuary emigration, we assume 85 to 95% survival based on studies in other systems (e.g., Scheuerell et al. 2009; Michel 2010; Dietrich et al. 2016).

Table 41. Yearling survival by location after overwintering. The Klamath River survival rate comes from the 2022 to 2023 JSATS survival study from the Hoopa Tribe.

Location	Yearling Survival
Klamath	0.92
Estuary	0.90

LFA Rules and Model Logic Overview

The following section provides an overview of the model logic (Steps) that feed into the LFA testing described in the next section. Following these steps below, we arrive at the abundance of juveniles that enter the ocean by size class and timing bin.

STEP 1: Assign Downstream Environmental Regime by Timing Class (Selecting Inputs)

Inputs: Abundance by size and timing class from Trinity River rearing and outmigration life stage and selected flow scenario (Klamath and Trinity flow conditions):

- Temperature regime (Cool, Nominal, Warm, Extreme; Table 36)
- Disease pressure category (None, Elevated, High; Table 37)
- Klamath Exposure (Table 38)

Calculation(s): For each timing class, downstream environmental conditions are assigned based on:

- Seasonal progression relative to emergence timing
- Flow scenario effects on temperature, exposure duration, and disease context

These assignments determine the survival multipliers applied downstream.

Outputs: Environmental regime attributes (temperature, exposure, disease context) for each size and timing group.

STEP 2: Apply Temperature-Related Survival Multiplier

Inputs: Juvenile abundance by size and timing class from (and input from Step 1 for non-estuary rearing juveniles), assigned downstream temperature regime.

Calculation(s): Apply a temperature survival multiplier (S_t) reflecting physiological stress associated with the assigned regime (Table 36). This multiplier applies uniformly across size classes but differs by timing class via regime assignment.

Outputs: Post-temperature-filtered juvenile abundance by size and timing class.

STEP 3: Apply Exposure Duration / Migration Timing Survival Multiplier

Inputs: Post-temperature juvenile abundance (output from STEP 2), size and timing class of juveniles, flow-dependent exposure regime.

Calculation(s): Apply an exposure duration multiplier (S_e) representing cumulative risk associated with (Table 38):

- Travel time
- Holding and residence
- Duration of thermal and disease exposure

Larger size classes receive higher S_e values due to reduced exposure duration.

Outputs: Post-exposure-filtered juvenile abundance by size × timing class.

STEP 4: Apply Disease-Related Survival Multiplier (Conditional)

Inputs: Post-exposure juvenile abundance (STEP 3), Disease pressure category assigned in Step 1, size class of juveniles.

Calculation(s): Apply a disease survival multiplier (S_d) only when disease pressure is elevated or high (Table 37). Disease effects compound temperature and exposure effects and are size-dependent.

Outputs: Juvenile abundance by size and timing class remaining after downstream survival filtering.

STEP 5: Apply Optional Estuarine Growth (Conditional)

Inputs: Juvenile abundance by size and timing class, estuarine growth scenario, estuarine temperature and disease conditions.

Calculation(s): Estuarine growth is applied only if a fry is less than 45 mm (Table 40).

Outputs: Updated juvenile abundance by size and timing class, prior to survival filtering.

STEP 6: Yearling Survival

Inputs: Trinity River yearling outmigrants after overwintering.

Calculation(s): Apply survival to remaining yearlings for the Klamath River and estuary (Table 41).

Outputs: Yearlings emigrating to the ocean.

STEP 7: Generate Ocean-Entry Cohorts

Inputs: Juvenile abundance by size and timing class following all survival filters, including yearlings.

Calculation(s): Surviving juveniles are transferred unchanged into the ocean entry life stage by size bins. No further size, timing, or survival modifications are applied at this boundary.

Outputs: Ocean entry abundance by size and timing class, passed directly to the First-Ocean-Year survival stage.

Conceptual Basis for LFA Testing:

The LFA for this life stage is designed to evaluate whether emigrating juvenile survival through the lower Klamath River and estuary migration corridor constitutes a dominant bottleneck to recovery, even when juvenile production and size structure from the Trinity River are favorable. Unlike upstream life stages that govern formation through growth and habitat capacity, this stage functions primarily as a selection and filtering phase, where survival outcomes are strongly conditioned by downstream environmental context rather than additional production.

Within the model framework, survival during Klamath outmigration is determined by the interaction of three primary mechanisms: (1) temperature regime, which establishes the baseline physiological stress experienced during migration; (2) exposure duration, governed by migration timing, travel time, and flow conditions; and (3) disease pressure, which acts as a conditional stressor that compounds temperature- and exposure-related mortality under biologically plausible conditions. Juvenile size inherited from Trinity River rearing influences survival indirectly by reducing exposure duration and increasing resilience, rather than through continued downstream growth. Optional estuarine rearing is treated as a conditional mechanism that may convert a limited fraction of early fry migrants into larger size classes under favorable conditions but is not assumed by default.

The LFA framework for this stage therefore focuses on determining whether downstream survival filters overwhelm upstream gains, whether improvements in Trinity River-produced size and timing propagate through to ocean entry under baseline or improved conditions, and whether coordinated management actions (e.g., flow, temperature, disease mitigation, timing shifts) can meaningfully reduce downstream losses. By isolating downstream selection processes from upstream formation and downstream marine survival, this life stage allows clear diagnostic evaluation of where recovery leverage resides within the basin.

Test 1: Is juvenile outmigration through the lower Klamath River and estuary migration corridor the primary limiting factor on ocean entry under baseline conditions?

Hypothesis: Juvenile Chinook salmon survival during juvenile outmigration through the lower Klamath River and estuary migration corridor constitutes a primary limiting factor on ocean entry, such that the number of juveniles entering the ocean is strongly constrained by downstream temperature, exposure, and disease conditions, even when Trinity River juvenile production and size structure are favorable.

Approach: Apply baseline conditions across the entire model.

Under these conditions:

- Propagate juveniles through the lower Klamath River and estuary migration corridor using the baseline temperature, exposure duration, and disease survival multipliers.
- Quantify cumulative survival to ocean entry by size and timing class (number of surviving individuals at the end of each transition).

- Compare downstream abundances to upstream juvenile abundance to evaluate whether downstream mortality substantially constrains ocean entry.

This test isolates the migration corridor as a survival filter under current or representative conditions, without confounding effects of upstream production variation or downstream mitigation actions.

Diagnostics and Interpretation:

1. Large losses across most size classes resulting in substantially reduced ocean entry → Juvenile outmigration is a primary limiting factor under baseline conditions.
2. Moderate losses with strong size-selective survival → Downstream survival interacts with upstream formation processes but does not impose an absolute ceiling.
3. Limited downstream losses with little change in ocean entry across size classes → Juvenile outmigration is not limiting under baseline conditions; constraints likely occur upstream or later in the life cycle.

Management Interpretation:

This test determines whether the lower Klamath River and estuary function as a dominant survival bottleneck under current conditions. If downstream survival substantially limits ocean entry even with adequate Trinity River production, recovery will require downstream interventions (e.g., temperature, flow, disease mitigation) rather than upstream restoration alone.

Test 2: Are downstream temperature, flow, and disease regimes sufficient to override upstream improvements in juvenile production and constrain adult escapement?

Hypothesis: Warm temperatures, low flows, and elevated disease pressure in the lower Klamath River can negate the benefits of improved Trinity River juvenile size, timing, and abundance, such that downstream environmental context ultimately determines adult escapement through its effects on ocean entry.

Approach: Apply the same Trinity River juvenile outmigration outputs (fixed size and timing structure) to contrasting downstream environmental regimes, including:

- Cool/high-flow, low-disease conditions
- Nominal conditions
- Warm/low-flow conditions with elevated disease pressure

Under these conditions:

- Propagate juveniles through each downstream regime using regime-specific temperature, exposure, and disease multipliers.
- Compare adult escapement across downstream regimes to evaluate the sensitivity of upstream improvements to downstream stress.

This test explicitly diagnoses whether downstream conditions dominate adult escapement outcomes, regardless of upstream juvenile production and size structure.

Diagnostics and Interpretation:

1. Downstream losses negate upstream improvements across all regimes → Downstream survival during juvenile outmigration is structurally limiting to adult escapement.
2. Upstream improvements persist only under favorable downstream conditions → Coordinated basin-scale management is required to realize escapement gains.
3. Upstream improvements persist under most regimes → Juvenile outmigration is not the dominant constraint on adult escapement.

Management Interpretation:

This test identifies whether recovery success, as measured by adult escapement, is contingent on favorable downstream years or management actions. If downstream conditions override upstream gains, recovery will require explicit management of flow, temperature, and disease risk in the lower Klamath River in addition to Trinity River restoration.

Test 3: Can increased Trinity River juvenile production compensate for downstream Klamath River mortality and achieve recovery targets?

Hypothesis: If juvenile outmigration imposes substantial mortality, increases in Trinity River juvenile production may or may not be sufficient to compensate for downstream losses and achieve adult escapement targets.

Approach: Under a representative downstream scenario identified as limiting in Tests 1 and 2:

- Incrementally scale Trinity River juvenile abundance (e.g., +25%, +50%, +100%) while preserving size and timing structure.
- Propagate scaled abundance through identical downstream survival logic.
- Pass resulting ocean-entry cohorts through first-ocean-year and adult return stages to evaluate escapement outcomes.

This test is diagnostic rather than prescriptive and does not assume scaled production is biologically achievable.

Diagnostics and Interpretation:

1. Escapement targets not achieved even with large production increases → Downstream limitation is non-compensable; recovery requires downstream intervention.
2. Escapement achieved only with unrealistically large increases → Downstream mortality imposes strong nonlinear filtering.
3. Escapement achieved with modest increases (≤25–50%) → Downstream limitation is compensable; Trinity restoration may be sufficient.
4. Diminishing returns with increasing production → Indicates nonlinear downstream survival constraints.

Management Interpretation:

This test distinguishes whether juvenile outmigration represents an absolute biological ceiling or a scalable constraint. If downstream mortality cannot be compensated by feasible increases in

Trinity production, management actions must focus on reducing downstream stress rather than further increasing juvenile output.

References

Apgar, T. M., J. E. Merz, B. T. Martin, and E. P. Palkovacs. 2020. Alternative migratory strategies are widespread in subyearling Chinook salmon. Ecology of Freshwater Fish 30:125–139.

Beamer, E. M., A. McBride, C. Greene, R. Henderson, G. Hood, K. Wolf, K. Larsen, C. Rice, and K. Fresh. 2005a. Delta and nearshore restoration for the recovery of wild Skagit River Chinook Salmon: Linking estuary restoration to wild Chinook Salmon populations. Supplement to the Skagit Chinook Recovery Plan. Skagit River System Cooperative.

Beechie, T., E. Buhle, M. Ruckelshaus, A. Fullerton, and L. Holsinger. 2006. Hydrologic regime and the conservation of salmon life history diversity. Biological Conservation 130(4):560-572.

Dietrich, J., K. Eder, D. Thompson, R. Buchanan, J. Skalski, G. McMichael, D. Fryer, and F. Loge. 2016. Survival and transit of in-river and transported yearling Chinook salmon in the lower Columbia River and estuary. Fisheries Research 183:435-446.

Healey, M. C. 1980. Utilization of the Nanaimo River estuary by juvenile Chinook salmon, *Oncorhynchus tshawytscha*. Fishery Bulletin 77:653–668.

MacFarlane, R. B. and E. C. Norton. 2002. Physiological ecology of juvenile Chinook salmon (Oncorhynchus tshawytscha) at the southern end of their distribution, the San Francisco Estuary and Gulf of the Farallones, California. Fishery Bulletin 100:244–257.

Mantua, N., I. Tohver, and A. Hamlet. 2010. Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. Climatic Change 102(1):187-223.

Michel, C. J. 2010. River estuarine survival and migration of yearling Sacramento River Chinook Salmon (Oncorhynchus Tshawytscha) smolts and the influence of environment. Doctoral dissertation. University of California, Santa Cruz.

Moore, J. W., J. Gordon, C. Carr-Harris, A. S. Gottesfeld, S. M. Wilson, and J. H. Russell. 2016. Assessing estuaries as stopover habitats for juvenile Pacific salmon. Marine Ecology Progress Series 559: 201–215.

Pickard, D., J. Alvarez, K. De Juilio, L. Gogan, J. Lee, K. Lindke, S. Naman, C. Smith, N. Som, and P. Zedonis. 2023. Trinity River Restoration Program: Science Plan. Trinity River Restoration Program. Available: https://www.trrp.net/library/document?id=2605.

Plumb, J. M., R. W. Perry, N. A. Som, J. Alexander, and N. J. Hetrick. 2019. Using the stream salmonid simulator (S3) to assess juvenile Chinook salmon (Oncorhynchus tshawytscha) production under historical and proposed action flows in the Klamath River, California (No. 2019-1099). US Geological Survey.

Plumb, J. M., R. W. Perry, N. A. Som, D. H. Goodman, A. C. Martin, J. S. Alvarez, and N. J. Hetrick. 2023. Calibration of the Trinity River Stream Salmonid Simulator (S3) with extension to the Klamath River, California, 2006–17 (No. 2023-1023). US Geological Survey.

Ray, R. A., R. A. Holt, and J. L. Bartholomew. 2012. Relationship between temperature and Ceratomyxa shasta–induced mortality in Klamath River salmonids. The Journal of Parasitology 98(3):520-526.

Richter, A. and S. A. Kolmes. 2005. Maximum temperature limits for Chinook, coho, and chum salmon, and steelhead trout in the Pacific Northwest. Reviews in Fisheries Science 13(1):23-49.

Scheuerell, M. D., R. W. Zabel, and B. P. Sandford. 2009. Relating juvenile migration timing and survival to adulthood in two species of threatened Pacific salmon (Oncorhynchus spp.). Journal of Applied Ecology 46(5):983-990.

Wallace, M. and B. W. Collins. 1997. Variation in use of the Klamath River estuary by juvenile Chinook salmon. California Fish and Game 83(4):132–143.

Wedemeyer, G. A., R. L. Saunders, and W. C. Clarke. 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. Marine Fisheries Review 42:1–14.

Zabel, R. W. and J. J. Anderson. 1997. A model of the travel time of migrating juvenile salmon, with an application to Snake River spring chinook salmon. North American Journal of Fisheries Management 17(1):93-100.

OCEAN REARING AND MATURATION TO RIVER ENTRY INTO KLAMATH RIVER

Description of Life Stage Transition:

This life stage represents ocean adult maturation and immigration. At this point, the juveniles have survived to ocean entry, where they will mature and return to the Klamath River as adults. This life stage transition relies on knowing the number of fish that enter the ocean from the previous life stage and survive to Klamath River entry to begin adult immigration. For this life stage transition, we assume that ocean habitat is not capacity limited (and therefore there are no capacity functions for this life stage transition), and we consider the following rule sets to determine the number of adults that survive from ocean entry to Klamath River entry:

- Size-selective first-ocean entry year survival rates with entry timing and ocean conditions and first ocean year conditions
- Age-specific ocean impact (harvest rates)
- Age-specific ocean survival (predation, ocean productivity, etc.)
- Age-specific maturation rates
- Age-specific straying rates

Assumptions for LFA and LCM Rules:

First Year Ocean Survival (Size): Survival during the first ocean year is influenced by both size and timing of ocean entry. Satterthwaite et al. (2014) reported that survival generally increases with fish size at ocean entry, with particularly strong gains in survival observed for fish entering the ocean at approximately 80 to 110 mm fork length. Based broadly on Lindley et al. (2009), baseline first-year ocean survival for Klamath-Trinity Chinook salmon populations was assumed to range from 1.5% under poor ocean conditions to 3.5% under favorable ocean conditions. Survival within this range was adjusted using ocean-entry size classes (Table 42). Although the general relationship between size and marine survival is well supported, no published study was identified that provides a direct empirical survival function or size-specific survival estimates for the size classes used in Table 42. Size-specific survival multipliers were developed using a literature-informed calibration approach intended to account for the influence of juvenile size at ocean entry on first-ocean-year marine survival from CDFW hatchery release-size conventions and professional judgment rather than direct outputs from a single empirical study.

Table 42. Size categories at ocean entry and survival multipliers for first ocean entry year.

Size Bin (mm)	Biological Justification	Size Multiplier (θ)
< 50 mm	Very small; below optimum; extremely high mortality; many fish delay in estuary. Assumed to all be subyearling migrants.	0.05
50–75 mm	Small; improved predator evasion vs <50 mm; low–moderate survival. Assumed to all be subyearling migrants.	0.40
75–100 mm	Smolted/preferred; strong improvements; moderate–high survival. May be comprised of late-timed subyearling migrants as well as yearling migrants.	0.80

Size Bin (mm)	Biological Justification	Size Multiplier (θ)
100–110 mm	Transition zone; step-up into high-survival regime. May be comprised of late-timed subyearling migrants as well as yearling migrants.	0.95
>110 mm	Largest sizes; consistently highest survival and early-marine growth. May be comprised of late-timed subyearling migrants as well as yearling migrants.	1.00

First Year Ocean Survival (Timing): Ocean-entry timing was also assumed to influence survival. Entry well before the spring transition was associated with reduced survival, whereas survival was assumed to be greatest for fish entering the ocean approximately 90 days after the spring transition. Survival then declined for progressively later entrants, although estimates for very late entry remain uncertain because of limited empirical data. Consistent with Satterthwaite et al. (2014), timing effects were assumed to be smaller than the influence of annual ocean conditions, which can overwhelm survival differences associated with entry timing alone. Ocean-entry timing relative to the spring transition was therefore used to adjust first-year ocean survival (Table 43). The multipliers in Table 43 were developed using expert biological judgment, with the literature used to support the direction and relative magnitude of the effects rather than the exact numeric values. The values should be interpreted as literature-informed scenario assumptions for sensitivity testing and model calibration, not as empirically estimated survival rates.

Table 43. Timing of ocean entry categories relative to spring transition date and survival multipliers.

Timing Category	Biological Justification and Description	Multiplier (τ)
Early (-2 to +4)	Well before the spring transition. Represents fish entering the ocean before favorable spring-transition conditions. Often associated with reduced survival.	0.70
Core (+5 to +10)	0–45 days after spring transition. Captures fish entering shortly after the transition when conditions are improving. Treated as baseline timing without penalty or boost. Your document notes that timing effects exist but are modest relative to ocean-year variability.	0.85
Late (+11 to +16)	46-134 days after spring transition. Represents the peak marine survival window and provides a small positive adjustment consistent with empirical evidence that size dominates early-marine survival, while timing provides secondary modulation.	0.98
Very late (+17 to +22)	≥135 days after spring transition. Slight survival penalty for late entries with conditions becoming less favorable.	0.85

First Year Ocean Survival (Ocean Conditions): Overlaid with size-selective and timing-gated survival, ocean productivity in the first ocean entry year can be a strong driver of survival to Ocean Age 2. Ocean-condition effects should be treated as a broad first-ocean-year survival modifier, with favorable conditions set to 1.0, neutral conditions retained at 0.8, and unfavorable conditions reduced to 0.5 (Table 44). The lower unfavorable multiplier is justified because poor ocean conditions off the California coast can produce nonlinear reductions in Chinook salmon marine survival, not merely small incremental declines from neutral conditions. In the California Current, warm ocean conditions, delayed upwelling/spring transition, poor prey availability, and altered food-web structure can sharply reduce juvenile growth and early marine survival. The

collapse of Sacramento River fall-run Chinook salmon associated with the 2004 to 2005 broods provides a strong California example, where poor ocean conditions were identified as a primary driver of record-low adult returns and fishery closures (Lindley et al. 2009). Therefore, an unfavorable multiplier of 0.5 represents a defensible midpoint for poor ocean years, while a sensitivity range of 0.4 to 0.6 can be used to evaluate uncertainty around the strength of the ocean-survival bottleneck.

While the literature supports the importance of ocean conditions as a major determinant of marine survival, no Trinity River-specific relationship exists that directly translates ocean conditions into survival multipliers. Consequently, the favorable (1.0), neutral (0.8), and unfavorable (0.5) multipliers were developed using professional judgment as part of the Trinity River life-cycle modeling framework. These values were selected to represent the relative differences in survival expected among productive, average, and poor ocean years while remaining consistent with the magnitude of survival variability documented in California Chinook salmon populations. The multipliers should therefore be interpreted as scenario-based calibration factors rather than direct empirical estimates.

Table 44. Ocean productivity and condition index categories and survival adjustment multipliers. Note only one of these options may be selected at a time.

Category	Survival Multiplier (κ)	Biological Justification and Description
Favorable	1.00	Cold/productive ocean conditions; strong prey availability and high expected marine survival.
Neutral	0.80	Baseline conditions. Mixed or average ocean conditions; moderate survival penalty relative to favorable years.
Unfavorable	0.50	Poor California Current conditions; warm ocean, weak upwelling, poor prey fields, and elevated risk of cohort failure.

Combining the size, timing, and ocean conditions survival multipliers, we have the abundance of Age 2 Chinook salmon and can apply age-specific harvest rates, age-specific ocean survival rates, age-specific maturation rates, age-specific stray rates, and proportion by run type (spring-run and fall-run) to calculate the number of adults entering the Klamath River by age-class and run type. The age-specific rates are described in detail below.

First Year Ocean Survival (Yearlings): Yearlings are assigned a relative first-ocean-year survival of 0.80 to represent their larger size, advanced smolt development, and expected survival advantage over most subyearling migrants. The value is a literature-informed calibration assumption, not an empirical estimate of absolute survival from ocean entry to Age 2, and should be evaluated through sensitivity analysis. Yearlings are not tracked by size and entry timing, which is why they do not have survival multipliers for size, timing entry, and ocean conditions. The survival of 0.80 encompasses all of those components into one value.

Ocean Harvest: Age-specific harvest is used in this model (Table 45; use 1-impact rate to calculate fish surviving harvest). We assigned age-specific ocean harvest rates of 50%, 55%, 50%, and 65% for Age 2 through Age 5 Chinook salmon, respectively. These values were used as expert-derived values based on overall Central Valley Chinook salmon ocean exploitation rate across adult age classes, rather than as empirically estimated age-specific rates. The assumed

rates are consistent with published estimates showing that Central Valley fall-run Chinook salmon ocean harvest rates have historically been on the order of 50 to 70%, including an average harvest rate of approximately 66% during 1967 to 1991 and exploitation estimates near 0.50 for Sacramento River fall-run Chinook salmon (Cramer and Ackerman 2009). More recent cohort reconstructions further indicate that fishery effects vary by cohort, age, and year, reinforcing that fixed age-specific rates should be interpreted as model assumptions (Chen et al. 2024). The model also has a minimum total ocean abundance threshold (10,000 individuals) that reduces harvest to 0.00 to simulate harvest management related to fish abundance.

Table 45. Ocean impact or harvest rates by age class, with default being derived from Central Valley fall-run chinook.

Age-class at End of Ocean Rearing	CACB Harvest Rates (Baseline Values)
Age 2	0.5
Age 3	0.55
Age 4	0.50
Age 5	0.65

Ocean Maturation: Ocean maturation rates come from the Klamath-Trinity fall-run Cohort Reconstruction Model (CRM) provided by the TRRP (Table 46**Error! Reference source not found.**). These are age-specific rates from the natural fish population. These rates calculate the number of adults returning to the river mouth before straying.

Table 46. Age-specific maturation rates from Klamath-Trinity fall-run Cohort Reconstruction Model for natural origin fish.

Age-class at End of Ocean Rearing	Maturation Rate
Age 2	0.055
Age 3	0.323
Age 4	0.756
Age 5	1.000

Ocean Straying: Age-specific ocean straying rates come from the Klamath-Trinity fall-run cohort reconstruction model provided by the TRRP (Table 47). These rates determine the number of adults that enter the Klamath River by age after applying the impact and maturation rates.

Table 47. Age-specific stray rates from the Cohort Reconstruction Model based on hatchery Klamath-Trinity fall-run Chinook salmon.

Age-class at End of Ocean Rearing	Straying Rate
Age 2	0.007
Age 3	0.008

Age-class at End of Ocean Rearing	Straying Rate
Age 4	0.012
Age 5	0.020

Spring and Fall-Run: The model does not track spring and fall run individually after emergence from the gravel. Using Junction City and Willow Creek weir data from 1980 to 2023, the proportion of spring- and fall-run returns were calculated (Table 48). The mean proportion was used as the baseline model input.

Table 48. Proportion by run type (spring-run and fall-run) from weir data from 1980 to 2023.

Run-Type	Mean Proportion (1980-2023) (Baseline)	Min Proportion (1980-2023)	Max Proportion (1980-2023)
Spring-run	0.4	0.79	0.07
Fall-run	0.6	0.21	0.93

Ocean Survival (Age 3-5): Ocean survival for adults Age 3 through 5 came from the Klamath-Trinity fall-run cohort reconstruction model provided by the TRRP (Table 49). The survival rates take into account ocean condition regimes based on the Sacramento River Fall Chinook Cohort Reconstruction Model (Chen et al. 2024). The baseline model uses the fair ocean conditions survival rates. The survival rates should be interpreted as scenario-based life-cycle model inputs derived from the best available regional information rather than direct estimates of Trinity River-specific marine survival.

Table 49. Ocean survival rates by age class from Cohort Reconstruction Model with modifiers for ocean condition regimes (Chen et al. 2024).

Age-class at End of Ocean Rearing	Survival Rate with Good Ocean Conditions (SR)	Survival Rate with Fair Ocean Conditions (SR) (Baseline)
Age 3	0.72	0.65
Age 4	0.72	0.65
Age 5	0.72	0.65

LFA Rules and Model Logic Overview

The following section provides an overview of the model logic (Steps) that feed into the LFA testing described in the next section. Following these steps below, we arrive at age-specific adult abundances by run type that survived to enter the Klamath River mouth and begin upstream migration.

STEP 1: First marine year (ocean entry to Age2)

Inputs: Abundance of juveniles entering ocean from estuary by size class and timing category (Time Step 0) and yearlings exiting the Klamath River.

Calculation(s): Multiply starting abundance of juveniles entering ocean among size and timing categories by survival baseline and multipliers for chosen ocean conditions for first ocean entry year. Apply yearling first ocean year survival, not dependent on size, timing, or ocean conditions (Baseline survival = 0.80).

Outputs: Abundance of Age 2 adults in ocean at beginning of Time Step 1. This is a combination of the Trinity rearing fish and yearlings.

STEP 2: Age2 ocean exploitation (harvest)

Inputs: Abundance of Age 2 fish after Step 1.

Calculation(s): Multiply by age-specific harvest rates as shown in Table 45 (use 1-impact rate to calculate fish surviving harvest).

Outputs: Abundance of Age 2 adults in ocean after harvest.

STEP 3: Age2 maturation

Inputs: Abundance of adults after Step 2.

Calculation(s): Multiply by age-specific maturation rate shown in Table 46.

Outputs: Abundance of Age 2 adults that return to Klamath River mouth before straying is accounted for (see Step 4).

STEP 4: Age2 straying

Inputs: Abundance of Age 2 adults at river entry after Step 3.

Calculation(s): Multiply by age-specific stray rate as shown in Table 47.

Outputs: Abundance of Age2 adults that enter the Klamath River mouth after straying is accounted for.

STEP 5: Split Age2 returning adults into spring-run and fall-run

Inputs: Abundance of Age 2 adults after Step 4.

Calculation(s): Multiply by proportion of fall-run and spring-run to allocate surviving juveniles to run type population.

Outputs: Abundance of Age 2 adults that enter the Klamath River mouth after straying is accounted for by each run type (fall-run and spring-run).

STEP 6: Holdovers from Age2 (remain at sea)

Inputs: Abundance of adults that did not mature in Step 3.

Calculation(s): Multiply by inverse of age-specific maturation rate (1-maturation rate) as shown in Table 47.

Outputs: Abundance of Age 3 adults that remain in ocean before harvest and survival are accounted for.

STEP 7: Age3 ocean survival and exploitation

Inputs: Abundance of adults from Step 6.

Calculation(s): Multiply by inverse of age-specific harvest rate (1-harvest rate) from Table 45 and age specific survival rate from Table 49.

Outputs: Abundance of Age 3 adults that remain in the ocean after harvest and survival are accounted for.

STEP 8: Age3 maturation, straying, and run breakdown

Inputs: Abundance of adults after Step 7.

Calculation(s): Multiply by Age 3 maturation rate shown in Table 46 and the inverse of Age 3 straying rate (1-straying rate) to determine the number of Age 3 adults entering the Klamath River. Portion the resulting Age 3 adults into each run type from Table 48.

Outputs: Abundance of Age 3 adults that enter the Klamath River mouth by run type.

STEP 9: Holdovers from Age3

Inputs: Abundance of adults that did not mature in Step 8.

Calculation(s): Multiply by inverse of age-specific maturation rate (1-maturation rate) as shown in Table 47.

Outputs: Abundance of Age 4 adults that remain in ocean before harvest and survival are accounted for.

STEP 10: Age4 ocean survival and exploitation

Inputs: Abundance of adults from Step 9.

Calculation(s): Multiply by inverse of age-specific harvest rate (1-harvest rate) from Table 45 and age specific survival rate from Table 49.

Outputs: Abundance of Age 4 adults that remain in ocean after harvest and survival are accounted for.

STEP 11: Age4 maturation, straying, and run breakdown

Inputs: Abundance of adults after Step 10.

Calculation(s): Multiply by Age 4 maturation rate shown in Table 46 and inverse of Age 4 straying rate (1-straying rate) to determine the number of Age 4 adults entering the Klamath River. Portion the resulting Age 4 adults into each run type from Table 48.

Outputs: Abundance of Age 4 adults that enter the Klamath River mouth by run type.

STEP 12: Holdovers from Age4

Inputs: Abundance of adults that did not mature in Step 11.

Calculation(s): Multiply by inverse of age-specific maturation rate (1-maturation rate) as shown in Table 47.

Outputs: Abundance of Age 5 adults that remain in ocean before harvest and survival are accounted for.

STEP 13: Age5 ocean survival and exploitation

Inputs: Abundance of adults from Step 12.

Calculation(s): Multiply by inverse of age-specific harvest rate (1-harvest rate) from Table 45 and age specific survival rate from Table 49.

Outputs: Abundance of Age 5 adults that remain in ocean after harvest and survival are accounted for.

STEP 14: Age5 maturation (forced), straying, and run breakdown

Inputs: Abundance of adults after Step 14.

Calculation(s): Multiply by Age 5 maturation rate shown in Table 46 and inverse of Age 5 straying rate (1-straying rate) to determine the number of Age 5 adults entering the Klamath River. Portion the resulting Age 5 adults into each run type.

Outputs: Abundance of Age 5 adults that enter the Klamath River mouth by run type.

Conceptual Basis for LFA Testing:

For this life stage transition, we compare contemporary adult returns and escapement under baseline conditions to established escapement and harvest objectives. The difference between baseline outcomes and these objectives defines the magnitude of the adult production deficit. We then systematically manipulate key biological, ocean, and management drivers to evaluate whether each factor alone, or in combination with others, can account for this deficit. This framework allows us to classify each factor as a primary limiting factor (alone sufficient to close the escapement gap under otherwise baseline conditions), a compounding limiting factor (important only in combination with other drivers), or non-limiting (present but not constraining outcomes), with respect to adult Chinook salmon returns to the Trinity River.

Fall-run Chinook Targets:

1. Increase escapement of naturally-produced fall-run Chinook salmon to 62,000 adults.
2. Population supports harvest (across all sectors) of 131,750 adults, conditional on meeting escapement objectives.

Spring-run Chinook Targets:

1. Increase escapement of naturally-produced spring-run Chinook salmon to 6,000 adults.
2. Population supports harvest (across all sectors) of 12,750 adults, conditional on meeting escapement objectives.

Test 1: Is harvest a primary limiting factor on adult escapement?

Hypothesis: Adult Chinook salmon escapement to the Trinity River is primarily limited by ocean and/or in-river harvest mortality, such that escapement targets can be met under baseline biological and ocean conditions if harvest mortality is sufficiently reduced or eliminated.

Approach: Use baseline model parameters. Systematically reduce ocean harvest rates by age class to zero while holding all other parameters constant. In a secondary scenario, eliminate both ocean and in-river harvest mortality. Evaluate resulting adult escapement to the Trinity River by run type relative to established escapement objectives.

Diagnostics and Interpretation:

1. Escapement targets met with ocean harvest eliminated alone → Ocean harvest is a primary limiting factor.
2. Escapement targets met only when both ocean and in-river harvest are eliminated → Combined harvest mortality is a primary limiting factor.
3. Escapement targets not met under zero harvest scenarios → Harvest is not a primary constraint and acts, at most, as a compounding factor.

Management Interpretation:

This test isolates the potential for harvest regulations alone to achieve recovery targets. If escapement targets are reachable through harvest reductions alone, management actions focused on harvest control could drive recovery without reliance on freshwater or ocean productivity

improvements. Failure to meet targets indicates that recovery requires addressing constraints earlier or later in the life cycle.

Test 2: Is early marine survival the dominant bottleneck?

Hypothesis: Adult Chinook salmon escapement is primarily limited by mortality during the first ocean year, such that escapement targets would be met under biologically plausible "good" early marine survival conditions even when harvest and later-life survival parameters are held at baseline levels.

Approach: Apply favorable, neutral (baseline), and unfavorable first-ocean-year survival conditions while holding harvest rates, later-age survival, maturation, and straying at baseline values. Compare resulting adult river entry and escapement to target benchmarks.

Diagnostics and Interpretation:

1. Escapement targets met under favorable early marine survival alone → Early marine survival is a *primary limiting factor*.
2. Escapement improves but remains below targets → Early marine survival is *compounding*, but insufficient on its own.
3. Minimal response to improved early survival → Constraints occur outside the first ocean year.

Management Interpretation:

This test determines whether recovery is fundamentally limited by conditions beyond freshwater management control. If early marine survival alone drives recovery, then freshwater actions may have limited leverage unless they substantially improve size and timing at ocean entry.

Test 3: Freshwater Production to Ocean Entry as a limiting factor on adult returns

Hypothesis: Adult Chinook salmon escapement is limited by insufficient juvenile production reaching the ocean, such that biologically realistic increases in the number of juveniles surviving to ocean entry—under favorable downstream and ocean conditions—can close the adult escapement gap.

Approach: Apply baseline conditions across the entire model.

Diagnostics and Interpretation

1. Large losses across most size classes resulting in substantially reduced abundance after ocean entry → Ocean entry is a primary limiting factor under baseline conditions.
2. Moderate losses with strong size-selective survival → Ocean entry conditions interact with upstream formation processes but do not impose an absolute ceiling.
3. Limited downstream losses with little change in ocean entry survival abundances across size classes → Ocean entry conditions are not limiting under baseline conditions; constraints likely occur upstream or later in the life cycle.

Management Interpretation:

This test evaluates whether recovery is plausible through cumulative improvements in freshwater rearing and downstream survival. If unrealistic increases in juvenile survival to ocean entry are required, recovery is primarily constrained by downstream or ocean processes rather than freshwater production alone.

Test 4: Is integrated recovery biologically plausible within TRRP influence?

Hypothesis: Recovery of spring- and fall-run Chinook salmon escapement is biologically plausible through combined, realistic improvements in freshwater production, size and timing at ocean entry, and early marine survival, without requiring extreme changes to any single process.

Approach: Simultaneously apply:

- Moderate increases in juvenile production to ocean entry,
- Improved size-at-entry and ocean-entry timing consistent with freshwater growth improvements, and
- Favorable but realistic first-ocean-year survival conditions, while holding harvest, later-life survival, maturation, and straying at baseline levels. Evaluate adult escapement outcomes relative to recovery targets.

Diagnostics and Interpretation:

1. Escapement targets met under combined moderate improvements → Recovery is *biologically plausible* within TRRP or adjacent influence.
2. Targets not met despite combined improvements → Downstream or ocean constraints dominate outcomes.
3. Recovery only achieved under extreme assumptions → Recovery is *not feasible* through integrated freshwater actions alone.

Management Interpretation:

This test frames realistic expectations for recovery planning. Successful outcomes indicate that coordinated freshwater actions can meaningfully contribute to recovery, while failure implies that ocean conditions or system-wide constraints fundamentally limit achievable outcomes.

References

Chen, E. K., Satterthwaite, W. H., O'Farrell, M. R., & Carlson, S. M. 2024. *Cohort Reconstruction for Sacramento River Fall Chinook Salmon and Comparison with the Sacramento Index.* Pacific Fishery Management Council methodology review document.

Cramer, S. P., and N. K. Ackerman. 2009. Effect of harvest rates on spawning escapement of fall Chinook salmon in the San Joaquin Basin. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* 1:88–100.

Lindley, S.T., Grimes, C.B., Mohr, M.S., Peterson, W.T., Stein, J.E., Anderson, J.J., Botsford, L.W., Bottom, D.L., Busack, C.A., Collier, T.K. and J.W. Ferguson. 2009. What caused the Sacramento River fall Chinook stock collapse. NOAA Technical Memorandum NMFS-SWFSC-447.

Satterthwaite, W.H., Mohr, M.S., O'Farrell, M.R., Anderson, E.C., Banks, M.A., Bates, S.J., Bellinger, M.R., Borgerson, L.A., Crandall, E.D., Garza, J.C., Kormos, B.J., Lawson, P.W. and Palmer-Zwahlen, M.L., 2014. Use of genetic stock identification data for comparison of the ocean spatial distribution, size at age, and fishery exposure of an untagged stock and its indicator: California Coastal versus Klamath River Chinook salmon. Transactions of the American Fisheries Society, 143(1), pp.117-133.