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APPENDIX A. DETAILED MODEL STRUCTURE AND TRANSITIONS

This appendix supports the Limiting Factors Analysis for Lower Trinity River Chinook Salmon (*Oncorhynchus tshawytscha*) Using the Hamilton and Murphy Method report prepared for the Trinity River Restoration Program. It describes the life cycle model (LCM) structure and transitions developed during Phase 1. The content is organized by Chinook Salmon life stage and transition, as shown in the revised conceptual life cycle diagram for Trinity River Chinook Salmon (Figure 1). Appendix B provides additional detail on model assumptions and input values; this appendix focuses on the life cycle and spatial structure of the LCM.

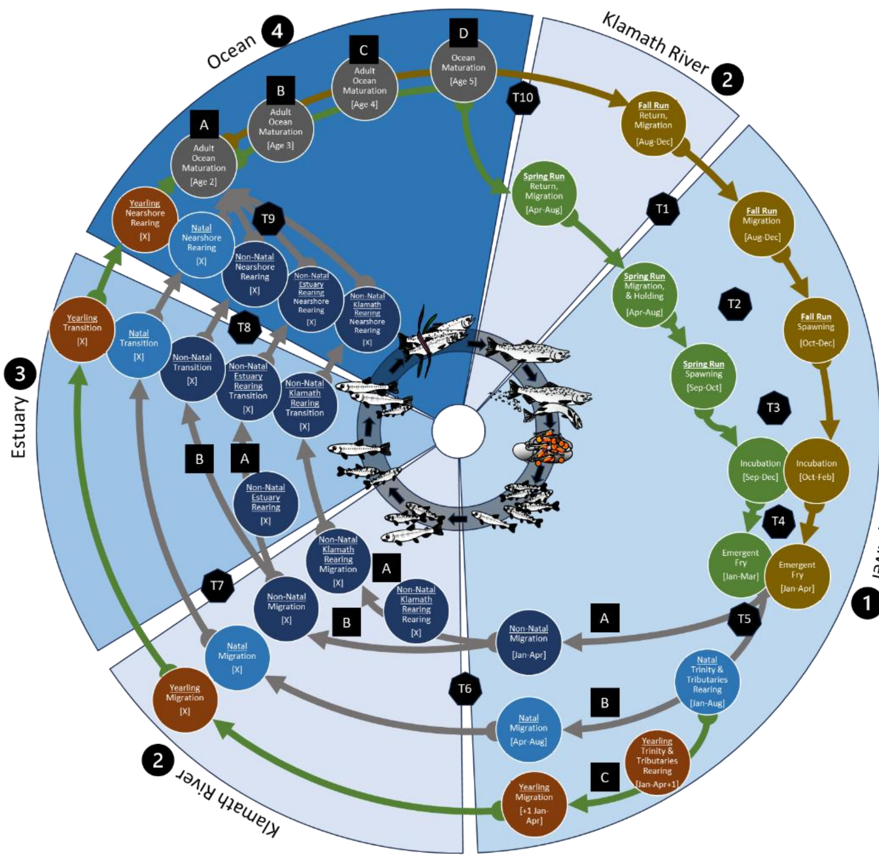

Figure 1. Revised life cycle diagram for Trinity River Chinook Salmon developed with TRRP scientists during Phase 1. The diagram shows the spatial structure as fish move through the Trinity River, Klamath River, estuary, and ocean. Life stages are shown as colored circles, with primary behavior and periodicity in brackets. Numbered arrows identify transitions between life stages and geographic areas, including alternative run-timing and juvenile life history pathways. Lettered black boxes identify alternative life history strategies described in the text. [X] indicates unknown periodicity or a value requiring further determination.

Key Life Stages

Chinook Salmon (*Oncorhynchus tshawytscha*) spend most of their life cycle in coastal Pacific waters but return to freshwater to reproduce. Their life cycle includes distinct freshwater stages that occur seasonally, particularly for fall-run fish. For concision, this section focuses on the freshwater stages and environmental factors most relevant to the LCM. Not all life history variants and population distinctions shown in Figure 1 are implemented at this time.

Upstream Adult — Although the mechanisms that trigger adult salmon to return to spawning grounds remain uncertain, navigation is thought to be influenced primarily by long-term olfactory memory (Dittman and Quinn 1996). Homing may also be supported by visual cues (Healey 1991), celestial navigation, magnetic orientation (Quinn 1980), and environmental changes in streamflow, turbidity, temperature, and dissolved oxygen (Allen and Hassler 1986). Unobstructed migratory routes are essential for adult migration. Predation, harvest, and water quality can affect an adult's ability to reach spawning sites and reproduce successfully (Hillemeier 1999; Beamsderfer 2000; Goniea et al. 2006). Anthropogenic impacts, including infrastructure, channel modification, flow diversion, and water quality degradation, can further impair migration to natal watersheds (Fisher et al. 1991).

The Trinity River supports both early-run timed Chinook Salmon (spring-run) and late-run timed Chinook Salmon (fall-run). Spring-run fish enter the river earlier (April–June) than fall-run fish (August–December), with little upriver migration from July–August (Rupert et al. 2017). Historically, these run types also used spatially distinct spawning grounds, as noted below (Kinziger et al. 2008). Based on TAG feedback, we assume that neither spring-run nor fall-run Chinook Salmon use the Klamath River for holding. Spring-run Chinook Salmon generally enter freshwater in an immature state and require deep pools with suitable conditions to complete maturation while conserving energy (Groot and Margolis 1991; Healey 1991). In contrast, fall-run adults typically enter freshwater in a more mature state and develop secondary sexual characteristics relatively quickly (Strange 2012; Hearsey and Kinziger 2015). They may still hold briefly in pools to conserve energy while awaiting conditions suitable for upstream migration and spawning (Groot and Margolis 1991; Healey 1991).

Spawning — Chinook Salmon generally spawn in stream gravels with a median diameter up to approximately 10% of body length (Kondolf and Wolman 1993). Female size and sediment size therefore influence site selection and redd construction success (Merz et al. 2024). Proximity to cover and shear zones provides refuge from predators and resting areas that aid energy conservation (Merz 2001; Wheaton et al. 2004). During spawning, females construct a redd, a depression formed by repeated body flexing that displaces gravel and fine sediment, coarsens the substrate, and creates a downstream mound of bed material (Crisp and Carling 1989). Multiple males often court a female, and fertilization may involve sperm from several males. Chinook Salmon are semelparous, spawning once before dying, although individuals may survive for days to weeks after spawning (Fleming and Gross 1990).

Fecundity and egg size vary among Chinook Salmon populations. For example, average fecundity is 5,423 eggs per female in the Mokelumne River (range: 2,132–9,492) and 7,423 eggs per female in the Sacramento River (range: 4,795–11,012) (Healey and Heard 1984; Kaufman et al. 2009). Density-dependent factors (e.g., disease, redd superimposition) and density-independent factors (e.g., temperature, flow) can influence spawning success and gamete viability (Patterson 2004; Tierney et al. 2009). Limited spawning habitat can lead to redd superimposition by later spawners, causing embryo mortality and a density-dependent relationship in which fry production declines as spawner density increases (McNeil 1964; Heard 1978; Buklis and Barton 1984; Parenskiy 1990; Chebanov 1991; Blankenship et al. 2024). In the Trinity River, spring-run and fall-run Chinook Salmon spawning was temporally and spatially separated before dam construction but now overlaps spatially, with some differences in timing (Kinziger et al. 2008; Rupert et al. 2017). Spring-run Chinook Salmon presently spawn from September–October, whereas fall-run Chinook Salmon spawn from October–December.

Incubation — After fertilization, female Chinook Salmon bury eggs within redds, where embryos develop in the gravel interstices. Egg burial depths, referenced to the original bed surface, can range from 5.5 to 51.5 cm, with means of 22.5 cm to the top of the egg pocket and 30 cm to the bottom (Evenson 2001). Incubation typically lasts 40 to 90 days, depending on water temperatures ranging from 4.4 to 12.2°C (Bams 1970; Heming 1982; Bjornn and Reiser 1991; Geist et al. 2006). Alevins remain in the gravel for 4 to 6 weeks after hatching, absorbing yolk-sac nutrients before emerging into the water column (Moyle 2002). Incubation success is closely linked to water temperature, dissolved oxygen, and substrate permeability (Merz et al. 2004). Gravel must be relatively free of fine sediment to support oxygen exchange, metabolic waste removal, and emergence (Tappel and Bjornn 1983; Chevalier et al. 1984; Groot and Margolis 1991). Contaminants, predation, and disease can further affect embryo and alevin development and survival (Merz et al. 2006; Merz et al. 2019).

At present, embryos incubating in Trinity River substrates represent a mix of spring-run and fall-run progeny, and parentage can only be determined through genetic analyses. As noted above, incubation duration depends on spawning date, temperature, and other factors. We generally describe incubation periodicity as September–December for spring-run progeny and October–February for fall-run progeny (Figure 1). Temperature variation and overlap in spawning timing can also produce variation in growth rates and size overlap during rearing and emigration (e.g., Merz et al. 2014).

Juvenile Rearing — Newly emerged juveniles typically use shallow, slow-moving habitats, then shift to deeper, faster water as they grow (Cramer and Ackerman 2009). Habitat complexity, including woody debris, overhanging vegetation, and seasonally inundated areas, provides refuge, resting areas, and feeding opportunities that support juvenile growth and survival. Juvenile diets vary by habitat but include terrestrial and aquatic invertebrates, larval fish, and eggs, particularly in California streams (Sasaki 1966; Merz and Vanicek 1996; Sommer et al. 2001). Prey size and consumption rates are influenced by juvenile size and water temperature (Merz 2002). Floodplain habitats can provide productive rearing conditions, including suitable temperatures, abundant prey, and protection from predators (Sommer et al. 2001; Jeffres et al. 2008). Habitat availability, water quality, temperature, and predation are key factors influencing juvenile rearing success (Lindley and Mohr 2003).

Emigration — Emigration timing and strategy are influenced by genetic factors, social cues, and environmental conditions during rearing and downstream migration. Juvenile Chinook Salmon emigrate as fry (<55 mm fork length [FL]), parr (>55 mm FL and <75 mm FL), or smolts (>75 mm FL) (Brandes and McLain 2001; Williams 2001; Zeug et al. 2014; Apgar et al. 2020). In the Trinity River, we describe three primary life history pathways: non-natal migrants, natal migrants, and yearling migrants (Figure 1; see Apgar et al. 2020). Non-natal migrants, or fry migrants, may spend only days to weeks in natal streams and therefore emigrate earlier and at smaller sizes than natal migrants. Natal migrants, or parr migrants, rear longer in natal streams (e.g., 1–6 months), feeding and growing before moving downstream. Yearlings overwinter in natal streams before emigration, although they may also rear in non-natal stream habitats or tributaries and typically leave the Trinity River between January and April in the year after emergence.

The proportion of emigrants in each stage can vary annually (Zeug et al. 2014). Although the contribution of fry emigrants to adult populations has been questioned (Brandes and McLain 2001; Williams 2001), recent studies show that fry-sized emigration can be a viable life history strategy (Miller et al. 2010; Sturrock et al. 2015). Flow, temperature, water quality, diversions, and predation are important determinants of emigration success (Cavallo et al. 2012; Notch et al. 2020). Smaller emigrants generally have lower survival because of size-selective mortality (e.g., Beamer et al. 2005a), but greater abundance of earlier, smaller migrants can compensate for lower individual survival. In some years and populations, non-natal survival rates can approach natal survival rates (e.g., Satterthwaite and Carlson 2015; Sturrock et al. 2015; Sturrock et al. 2019). Thus, both natal and non-natal rearing can contribute to population resilience and are included in the Trinity River conceptual life cycle diagram (Figure 1).

Ocean Maturation — As juveniles emigrate through freshwater habitats to the ocean, use of estuarine and shallow nearshore habitats varies among life histories. These habitats can support physiological transition to marine life and provide productive foraging habitat and refuge from predators (Hodgson et al. 2020). Salmon origin, size, and timing of ocean entry strongly influence survival and adult return success (Satterthwaite et al. 2013; Satterthwaite et al. 2014; Satterthwaite et al. 2015; Satterthwaite et al. 2017). Smaller, earlier fry migrants are more likely to rear for weeks to months in estuarine or shallow nearshore habitats (see Beamer et al. 2005a and 2005b for analogous patterns in Skagit River Chinook Salmon), whereas larger, later migrants may move quickly through these habitats to deeper offshore areas. Maturation rates vary with ocean productivity, ocean conditions, and harvest (Wells et al. 2007), with adults typically returning at age-2 to age-5. In the Trinity River, age-5 adults appear to make up a small portion of returns, while age-3 and age-4 adults dominate most years (Lindke 2021). Age-2 adults vary among years but can represent a substantial share of returns in some years (Lindke 2021).

Key Transitions

The following descriptions correspond to the transitions (T) shown in Figure 1. These transitions link life stages, spatial domains, and LFA tests and provide the structural foundation for the LCM.

T1 Adult migration from the Klamath River to Trinity River

Adult Chinook Salmon enter the Klamath River and migrate upstream to the Trinity River confluence. This transition includes both spring-run and fall-run adults and is influenced by migration conditions, water quality, harvest, and predation.

T2 Adult immigration, holding and spawning in Trinity River

This transition includes spring-run and fall-run adults after they enter the Trinity River and migrate upstream to spawning habitat, including any holding behavior. Relevant drivers include flow, temperature, passage conditions, holding habitat, energetic costs, and prespawn mortality.

T3 Adult spawning in Trinity River to incubation

This transition covers adult spawning and egg deposition in redds, which initiates incubation. Relevant drivers include spawning habitat availability, gravel quality, spawner density, redd superimposition, flow, and temperature.

T4 Incubation to emergent fry in Trinity River

This transition covers development from eggs deposited in redds through incubation and emergence as fry. Relevant drivers include temperature, dissolved oxygen, fine sediment, substrate permeability, scour, dewatering, disease, and contaminants.

T5 Emergent fry to rearing in Trinity River

This transition covers fry emergence and initial rearing in the Trinity River. Duration varies by life history pathway and is influenced by habitat availability, temperature, flow, food availability, competition, and predation.

T6 Trinity rearing to emigration from the Trinity River to Klamath River

This transition covers juveniles rearing in the Trinity River through emigration into the Klamath River. It includes multiple life history pathways with different rearing durations within the Trinity River (life history pathways A, B, and C in Figure 1). Relevant drivers include flow, temperature, habitat capacity, food availability, density dependence, diversions, and predation.

T7 Klamath River rearing and emigration to Klamath River estuary

This transition covers Trinity River juveniles after they enter the Klamath River, either for non-natal rearing or continued downstream migration to the estuary. It includes all three primary life history pathways (A, B, and C in Figure 1). Relevant drivers include Klamath River flow, temperature, water quality, disease, tributary rearing opportunity, migration distance, and predation.

T8 Klamath River estuary rearing and emigration to nearshore

This transition covers entry into the Klamath River estuary and movement to nearshore habitats. Some juveniles may rear for extended periods in estuarine or transitional habitats, whereas others may move through the estuary with little or no rearing. Relevant drivers include estuary habitat availability, salinity transition, temperature, food availability, residence time, and predation.

T9 Nearshore rearing to ocean rearing and maturation

This transition covers juveniles moving from nearshore habitats into ocean rearing and maturation, including movement from shallow nearshore areas to deeper offshore habitats and broader ocean migrations. Relevant drivers include ocean-entry timing, body size, ocean productivity, prey availability, predation, and harvest exposure.

T10 Ocean rearing and maturation to river entry into Klamath River

This transition covers mature adults leaving ocean habitats and entering the Klamath River through the estuary, beginning upriver migration. Relevant drivers include ocean survival, maturation schedule, harvest, river-entry timing, estuary conditions, and lower-river water quality.

Spatial Structure

The model includes a simplified spatial structure to distinguish where constraints may arise along the migration corridor. Spatial domains include the Lower Trinity River from Lewiston Dam to the Klamath confluence, the Klamath River from the Trinity confluence to the estuary, the Klamath River estuary and nearshore, and the ocean (Figure 1). Within the Trinity River, the model includes three primary reaches for escapement, spawning, and rearing. These reaches differ in geomorphic structure, rearing capacity, and thermal regime, which can influence juvenile growth, habitat competition, and emigration timing. The Trinity River reaches included in the model are:

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

This spatial structure supports interpretation of where mortality, reduced growth, or delayed development occurs and helps connect model results to management actions. It distinguishes constraints within the Trinity River from those arising downstream or in marine environments. The reach structure also aligns with key monitoring locations, including juvenile rotary screw traps and adult weirs, and with transitions among the Trinity River, Klamath River, estuary, and ocean (Figure 2).

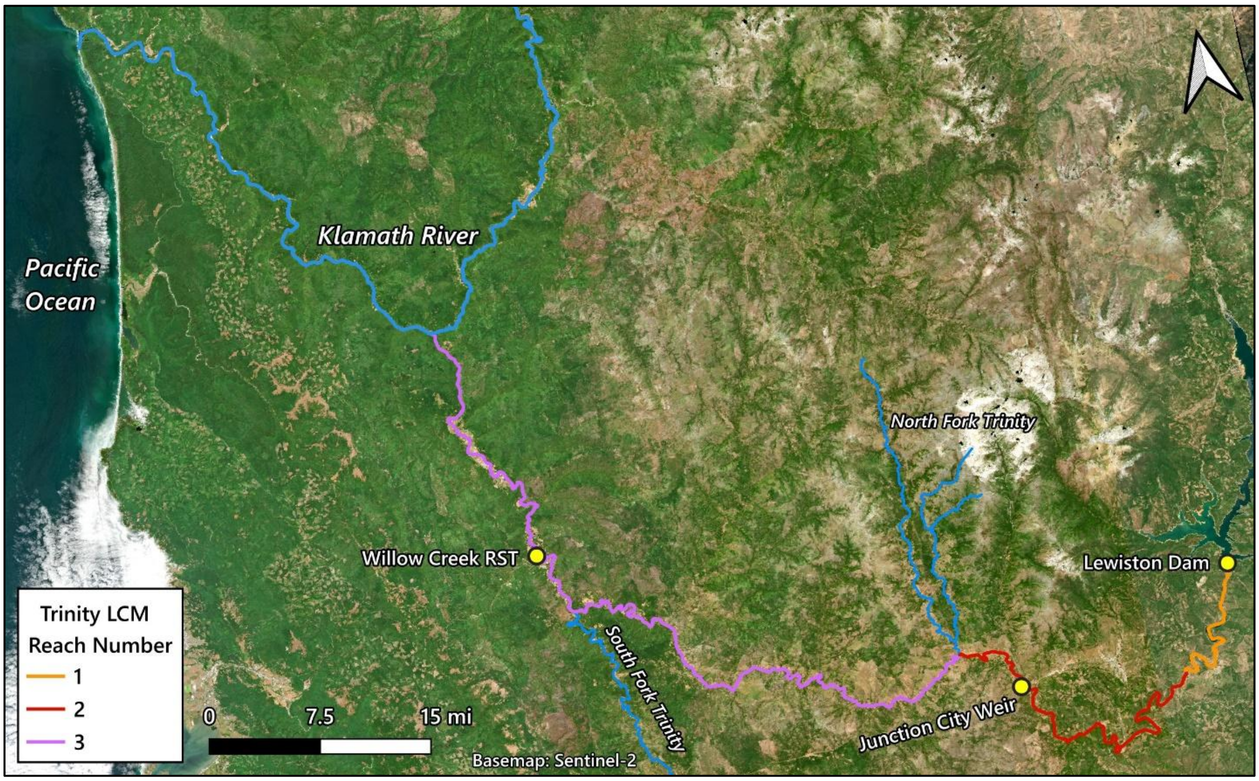

Figure 2. Study area and spatial structure for the Trinity River Chinook life cycle model and limiting factors analysis.

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