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ESHE: A Life-Cycle–Integrated Modeling Framework for Quantifying Salmon Rearing Habitat

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Abstract

Effective management of migratory species necessitates understanding habitat needs across space and time, yet quantifying these requirements remains challenging. We developed the Emigrating Salmonid Habitat Estimator (ESHE) model to estimate juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) rearing habitat needs and identify habitat deficits in a California Central Valley river where suitable habitat is limited. ESHE simulates emergence, rearing, and downstream migration of salmon cohorts on a daily timestep, incorporating size-dependent growth, migration rates, and territory requirements parameterized with river-specific data. By integrating ESHE outputs with high-resolution habitat availability models, we quantified spatial and temporal habitat deficits under varying flow and population scenarios to inform restoration priorities. Results indicated that habitat deficits were greatest in upper spawning reaches for the current population and intensified in the middle and lower reaches when modeling the population goal. Flow variation had minimal effect on habitat extent due to channel simplification and floodplain loss, emphasizing the need for restoration strategies that increase habitat quality and quantity during critical periods. Sensitivity analysis revealed that survival parameters exert the strongest influence on model outputs, underscoring the need for improved empirical estimates. ESHE provides managers a spatially and temporally explicit framework for identifying habitat bottlenecks, prioritizing restoration actions, and aligning flow management with juvenile salmon behavior. By linking habitat availability to population objectives, ESHE supports data-driven decisions that optimize resource allocation, reduce ecological risk, and advance recovery goals for migratory fish species that complete life cycles across multiple habitats.

1. Introduction

Flow regulation has escalated the degradation of global riverine ecosystems. Concomitant ecological, economic, and societal concerns are now driving large-scale conservation and rehabilitation efforts [33, 100, 11–12, 58]. These management responses, and their associated economic ramifications, have driven demand for predictive and reliable forecasting tools to measure resource population impacts and responses to management actions [16, 55, 31, 26]. While the field of ecology has successfully documented population responses to measured environmental change [e.g., 91, 37, 40], the ability to accurately forecast aquatic ecosystem reaction to future habitat modifications has been more elusive [44]. Addressing this challenge is key to optimizing the impact of limited restoration funds, but it requires a deep understanding of the dynamic relationship between habitat conditions and target species populations.

Accurately assessing population–habitat relationships is critical for conservation, resource management, and sustaining ecosystem services [97, 20–21]. For the restoration of degraded stream corridors and the development of large-scale, sustainable watershed strategies, it is vital for managers to consider the habitat needs of focal species throughout their life history. Managers must also work towards re-establishing the necessary quality and quantity of essential habitat features and the flows that activate them, allowing these species to not only survive but thrive [69, 74, 105].

A key concept in predicting a species' response to habitat alteration is that a population's size, growth rate, and behavior (e.g., spatial distribution, migration, rearing) are ultimately driven by a mosaic of spatially heterogeneous environmental covariates representing habitat quantity, quality, and connectivity (accessibility), as well as climatic conditions, resource availability, life history diversity, and risks [2, 43, 59]. The quality and quantity of physical habitat strongly influence the structure and composition of river biotic communities [57]. It is therefore consistent that these physical habitat conditions provide a framework for estimating ecological impacts from flow and non-flow alterations to streams [32]. While limitations in model predictions have been identified [93], physical habitat modeling coupled with habitat suitability criteria is now a commonplace method for quantifying available habitat for specific species and life stages of interest [125, 104, 83]. These models provide a framework for estimating aquatic habitat activation and adjustment from management actions [17, 127, 111].

However, to understand and manage population change through physical habitat modification, resource managers need to not only estimate habitat availability across space and time but also estimate how a population responds to this availability. To that end, managers often prioritize habitats using analyses that quantify how landscape factors influence patterns of habitat selection [47]. Although this approach has been successful for several species [15, 82], habitat use patterns are influenced by population size and density as well as ontogeny, behavior, and movement limitations. These factors, and those that affect habitat access, are much more difficult to consider in traditional habitat selection analyses. In complex systems, the long-term interactive influences of such factors may also change which habitats are important for species persistence [93]. These issues are further complicated when migratory species utilize specific habitats for only a portion of their lifecycles. This requires an understanding of how variation in demographic parameters at one life stage can affect behavior, survival, and ultimately population size at later life stages [103, 45].

The theory and techniques for watershed habitat quality analyses are well developed [89–90]. Some habitat assessment models link target population demographics to habitat quantity or quality, an especially useful approach if habitat characteristics are allowed to change over time. For example, Matthiopoulos et al. (2019) predicted population growth or decline from detailed habitat composition and selection for house sparrows (*Passer domesticus*). Nickelson (1998) developed functions relating Coho Salmon (*Oncorhynchus kisutch*) demographics to specific habitat features, which were used in a population viability analysis [78]. However, in these examples, habitat variations were modeled as a proportional change in the quantity or quality of habitat over time rather than landscape or habitat simulations.

Methods for aquatic habitat modeling based on flow simulations and population modeling based on habitat quantity or quality are both well developed, but we are not aware of published studies that effectively join them into a single, comprehensive analysis that predicts population response to changes in habitat quantity and quality (Fig. 1). We combined four elements of a habitat-based population response model into a single analysis to predict population needs for Chinook Salmon (*O. tschawytscha*) rearing habitat restoration planning, which we refer to as the Emigrating Salmonid Habitat Estimator

(ESHE) model. First, we used physical habitat and habitat suitability models to estimate habitat availability in space and time under a range of flow conditions [114, 29] (Fig. 1-1a). Next, we incorporated transferable habitat selection models to estimate the population distribution across habitats [126] (Fig. 1-1b). Then, we developed a framework connecting habitat use to concurrent population change data, incorporating behavioral (e.g., habitat occupation, migration) and demographic responses (e.g., growth, mortality) over time [86] (Fig. 1-2a). Finally, we incorporated a life cycle modeling component that predicts specific effects on one life stage (e.g., growth, movement, survival) on population size and health at a later life stage [121, 81] (Fig. 1-2b).

We demonstrated how models of habitat, flow modification, and other dynamic factors can be integrated into a coherent framework for predicting population trends. Chinook Salmon are a highly valued species that, similar to other anadromous salmonids, have experienced significant population declines across their native range, particularly in California [115, 113, 128]. Chinook Salmon are an ideal candidate for large-scale habitat-population modeling because freshwater spawning and rearing habitats have been identified as key limiting factors of population recovery. Additionally, most population monitoring and restoration efforts to date have focused on freshwater habitat [91, 34]. We applied a spatially explicit cohort-based model that is linked to physical habitat simulations using a high-resolution, two-dimensional habitat suitability model [71, 38, 116].

This framework, the ESHE model, simulates movement, growth, survival, and territory requirements of juvenile Chinook Salmon cohorts, allowing for estimation of rearing habitat needs across time and space to inform the spatial distribution and extent of additional habitat needed to sustain the current population, as well as target abundance levels. We derived the model from first principles, providing a strong theoretical foundation [50, 70, 92, 41]. We used the model to explore five scenarios designed to demonstrate different functionalities and potential applications. Furthermore, we used this quantitative link between habitat availability and change in population size to examine how targeted habitat rehabilitation approaches could be most effectively implemented to achieve the often elusive ecological objectives of restoration actions [89, 80]. To account for uncertainty and test prediction robustness, we conducted a sensitivity analysis, identifying which parameters most strongly influence model outputs and highlighting where improved data or monitoring would most reduce model uncertainty. Finally, we generated a web-based user interface allowing resource managers to use ESHE to visualize and predict reach-specific habitat needs (Access through Data Availability Statement).

We applied the ESHE approach to the following five scenarios, with the intent of assisting managers in habitat restoration planning under varying environmental conditions and population levels, and with the overarching goal of supporting long-term habitat maintenance and achieving population recovery. Specific simulation scenarios were run to estimate: (1) How rearing habitat deficit varies along the river corridor for the current returning adult population level across three relevant flow conditions; (2) How the rearing habitat deficit varies along the river corridor with the Central Valley Project Improvement Act (CVPIA) goal population of 160,000 returning adults (goal population) across three relevant flow conditions [25]; (3) How much habitat is needed across the rearing period at different time periods (e.g.,

February and April under spring base flow conditions); (4) How much rearing habitat is needed to support the current returning adult population (baseline scenario); and (5) How much rearing habitat is needed to support the goal population. Along with the five scenarios, we also include an example illustrating how the ESHE model can be applied to management and restoration planning by identifying river reaches with the greatest habitat deficits under different flow and population scenarios, while also producing population and individual-level metrics relevant to management decisions. Our aim is to demonstrate how the model can be used to assess the influence of managing for different migration strategies on the range of habitat needs, and to illustrate how the model can help managers prioritize restoration planning under varying environmental conditions.

2. Materials and Methods

2.1. Study Species

Chinook Salmon, like other Pacific salmon, are anadromous and semelparous, spending most of their lives in the ocean before returning to freshwater to spawn and die. Over their life span, California Central Valley (CV) Chinook Salmon migrate between CV river systems and the Pacific Ocean, with distinct life stages occurring during specific time periods. For example, adult immigration and spawning occur primarily from October through November, while juvenile rearing and emigration generally occur from February through June. Despite this general pattern, Chinook Salmon exhibit a wide range of life history strategies, including variation in age at seaward migration and duration of natal stream and freshwater residence. Their various strategies have important effects on size and survival at ocean entry [134, 2]. Comprehensive descriptions of CV Chinook Salmon life stages can be found in Healey (1991), Moyle (2002), and Williams (2006). For modeling purposes, we focused on the freshwater fry and parr life stages, which occur within the Lower American River (LAR; Fig. 1).

Once adults reach maturity, they leave the ocean to return to their spawning grounds. Following spawning, egg incubation generally lasts from 40 to 90 days at water temperatures of 4.4 to 12.2°C [48, 13, 39]. Incubation is highly dependent on water temperature, dissolved oxygen, and substrate permeability [62]. Fry commonly disperse downstream after emergence because weak swimming ability, reduced visual contact with the substrate—particularly under turbid conditions—and temperature-driven behavioral responses limit their capacity to orient, maintain position, and establish rearing territories near the natal site [1, 27]. As fry grow, their preferences change from shallow water to deeper habitats, which alters their spatial use and makes them more migratory than sedentary. During this transition, fry begin to establish and defend rearing territories. Features such as woody debris, overhanging vegetation, and seasonal inundation increase habitat complexity and provide more juvenile hiding, resting, and feeding habitat. The more complex the habitat, the greater ability juveniles have to grow, develop, and survive emigration. Off-channel habitats such as side channels and floodplains may provide better juvenile rearing opportunities because they expand rearing capacity and prey production within a reach and provide high flow and predator refuge [101, 99].

Juvenile Chinook Salmon exhibit both schooling behavior and exclusive space use, suggesting that territoriality plays a role in density-dependent regulation, even if they do not defend individual feeding territories as rigidly as resident salmonids [76]. While early studies assumed fixed territory sizes [52], more recent work shows that territory size decreases with density until a minimum threshold is reached [56], effectively limiting the number of individuals that can occupy a given habitat section. This supports evidence that freshwater rearing habitat is a major limiting factor for threatened Chinook Salmon populations [112, 131], and suggests that if juvenile abundance, body size, and location are known and behaviors accurately simulated, population-level habitat needs could be estimated based on assumptions about minimum space requirements.

The timing and stimuli for emigrants to leave a natal stream depend on individual genetics, social cues, and environmental factors to which individuals are exposed as they emerge, rear, and migrate downstream. Along the Pacific Coast of California, Chinook Salmon emigration size varies widely, but juveniles generally emigrate as non-natal (≤ 45 mm fork length [FL]) or natal (> 45 mm FL) rearing [2]. In some systems, the proportion of natal and non-natal salmon emigrating shifts inter-annually depending on flow variability and other factors [134, 65]. Flow, temperature, water quality, diversion, and predation have been implicated as key parameters that affect successful emigration [67, 135].

2.2 Study Area

The American River is the southernmost Sacramento River tributary and historically supported at least two runs of Chinook Salmon (spring and fall) and winter-run steelhead (*O. mykiss;* Fig. 2) [120]. The Sacramento River flows into the Sacramento-San Joaquin Delta (hereafter, the Delta), then into the Pacific Ocean. Like other CV rivers, the LAR is highly degraded due to anthropogenic modifications, including flow regulation and diversion, water pollution, gold and gravel mining, flood protection, and hydropower and floodplain development [73, 119]. The Folsom and Nimbus dams block coarse sediment input from the upstream watershed and exclude anadromous salmonids from ~ 80 to 100% of historic spawning grounds [128]. Natural anadromous steelhead and Chinook Salmon spawning and rearing still occur within the 36-km reach between Nimbus Dam and the Sacramento River confluence; however, the remaining habitat is degraded from lack of coarse sediment input, flow regulation, and levees [129]. To address this problem, the U.S. Bureau of Reclamation, U.S. Fish and Wildlife Service, and City of Sacramento have implemented LAR gravel augmentation and side channel and floodplain enhancement since 2008 as part of the CVPIA to rehabilitate degrading spawning and rearing sites [25]. To track management success, numerous monitoring programs have been implemented within the CV and coastal waters [65].

2.3. Habitat Availability

We quantified habitat availability across a range of LAR flows using submeter-resolution two-dimensional hydrodynamic model outputs, aerial imagery, and habitat suitability criteria derived from juvenile Chinook Salmon observations recorded during snorkel surveys conducted throughout the upper

12 river kilometers (RKM) of the LAR between 2022 and 2024. Details of the underlying hydrodynamic and habitat suitability modeling are available in CBEC Eco Engineering (2024).

In the model, habitat availability at each modeled flow represents the area currently suitable for juvenile Chinook Salmon rearing (present available habitat). To evaluate habitat requirements of specified population targets, we used the total wetted area at each modeled flow as an upper bound on available habitat (maximum potential habitat). Habitat availability was evaluated for a subset of modeled flows selected to represent ecologically relevant low (5%; 21 m^3/s), intermediate (50%; 71 m^3/s), and high (95% 425 m^3/s) flow conditions during the LAR juvenile rearing period (Jan to June), using daily flow (20 years; USGS Gage 11446500). The 2004 to 2024 interval best represents the current LAR flow management standards [94].

3. Emigrating Salmon Habitat Model

Building on the conceptual framework described above, the ESHE model simulates juvenile emergence, growth, movement, survival, and habitat occupancy along a regulated river corridor. ESHE simulates juvenile emergence, growth, survival, behavior, and downstream movement. Habitat occupancy is governed by habitat availability, fish size, and behavioral state, with individuals shifting behaviors and locations when capacity is exceeded in a given reach. Fish passing the downstream LAR boundary at the Sacramento River confluence exit the system as emigrants. This iterative daily process continues until all cohorts leave the system, capturing dynamic interactions between fish biology, behavior, and habitat constraints.

Our goal was not to realistically simulate all mechanisms controlling Chinook Salmon rearing and emigration behavior. Instead, we applied simplified, empirically supported relationships through space and time to estimate rearing habitat needs, using the LAR as a model system. A model's usefulness is measured by how well it captures the interactions of the most important factors and leaves out unimportant ones [36], thereby limiting model complexity that could make interpretation more difficult. Accordingly, our objective was to model Chinook Salmon emigration in the LAR with adequate complexity to capture key behavior and habitat use patterns. Model development is an iterative process that highlights data gaps and parameters requiring further refinement. The LAR ESHE model is intended to be updated as additional data become available.

The model was developed in R [88] and utilizes the dplyr package [117].

3.1 ESHE Model Components and LAR Application

Estimating the daily required habitat needs of the LAR juvenile Chinook Salmon population requires accurate information on fish body size, abundance, and minimum territory requirements as they migrate downstream (Table 1). The model's input parameters of adult abundance, spawning location and timing, and size define the initial number of fish, their spatial distribution, entry timing, and fork length.

Emigration parameters of survival, growth, and movement inform the daily survival, body size increase, and juvenile cohort speed as they emigrate through the LAR. Details on parameter values and data sources are described in the following sections.

The subsections below describe the assumptions and sequential steps of the ESHE model with the accompanying data. These are model constructs based on best available science, not definitive statements about LAR processes, except where explicitly stated. Unless noted otherwise, “model” refers to ESHE.

3.1.1 Spatial Habitat

The ESHE model requires habitat availability data, expressed as the area of suitable rearing habitat per RKM for the flows and species of interest. These data are essential for the model to determine cohort behavior and habitat occupancy within the system as capacity dictates fish movement. When a RKM is below capacity, fish will rear; when a RKM exceeds capacity, fish shift behavior and move downstream. Flow conditions may be specified as continuous for the entire simulation or varied at weekly or monthly intervals. In this application, flow is held constant for the duration of the simulation.

In the LAR application, the present available habitat (km^2) was calculated for juvenile Chinook Salmon by RKM using a combination of submeter-resolution two-dimensional hydrodynamic model outputs, aerial imagery, and habitat suitability criteria derived from snorkel survey data collected on the LAR [24].

3.1.2 Spawning and Emergence

Prior to model initialization, input data are required on redd distribution, emergence timing, fork length at emergence, and the proportion of fish emerging per day. The model is initialized with a user-specified number of returning adults, from which total fry production is estimated using river-specific fecundity and egg-to-fry survival rates, and an assumed sex ratio (Table 1). These estimates, combined with emergence timing and spatial redd distribution, determine the daily number of fry emerging within each RKM.

Following emergence, the cohort is redistributed downstream from the emergence location, simulating advection of fry prior to territory establishment [1, 27]. Cohorts are partitioned into natal and non-natal cohorts, using a user-defined fixed proportion for each model run. Non-natal fish are assigned the behavioral state *Migrating*, signifying them emigrating out of the system without rearing, a common behavior documented in the LAR and other CV tributaries [65, 106, 2]. Natal rearing cohorts are assigned to the behavioral state *Looking*, signifying an active search for available rearing habitat.

Spawning distribution data from LAR aerial photo surveys conducted two to three times annually from 2012 to 2023 [107, Reclamation unpublished data] were used to estimate the average proportion of redds at each RKM, per year. The average spawning proportion per RKM across years was used to represent the spawning distribution in the model (Fig. 3). Aerial photo data were used for this model component because they capture the full extent of spawning along the river continuum [119]. LAR

ground-based spawning surveys provide better temporal resolution as they are conducted more frequently (provide temporal resolution); however, they are typically conducted only at gravel augmentation sites and adjacent control reaches.

To estimate fry emergence, 2023 LAR spawning ground survey data were analyzed [108] (Fig. 4). Data from other years were collected at different times and intervals; standardizing multiple years together resulted in gaps and excessive extrapolation. The 2023 dataset was the most recent at the time this was written. It spans the entire spawning season at approximately three-week intervals, and was the most comprehensive, making it the best choice for modeling emergence timing. Raw data were used to determine the peak spawning day and overall shape of the spawning distribution. Using statistical methods within the truncnorm package, a truncated normal distribution was found to best represent the data, with start and stop dates matching the field data and a peak on the same day [61]. The resulting distribution was then used, along with daily mean temperature data from 2023 and early 2024, to estimate fry emergence timing based on the accumulation of 750 degree-days [98, 75, 6] (Fig. 4). The size of fish at emergence is derived from the mean size of yolk-sac fry observed in the LAR rotary screw trap [30]. Juvenile emergence timing and size at the emigration initiation are informed and calibrated by observations of emigrating juveniles captured by rotary screw traps downstream of the spawning grounds [30, 75, 6].

Following emergence, cohorts were redistributed across the emergence reach and the 5 RKM downstream extent (6 RKMs total) using a left-skewed beta distribution (Beta($\alpha = 6, \beta = 5$)). The distribution was applied to all cohorts and was scaled to each cohort's emergence reach and the downstream extent. This approach creates an asymmetric downstream displacement consistent with fry advection [1, 27].

The model calculates the number of emerging fry based on the user-defined number of adult returns (Eq. 1).

$$Fry = Spawners * SR * F * EF \quad (1)$$

The number of returning adults defaults to 22,930 returning adults, representing the 15-year (2009–2023) average of in-river LAR adult returns [3]. The equation assumes a sex ratio (SR) of 1:1, an average fecundity (F) of 6,001 eggs per female based on data collected by the California Department of Fish and Wildlife (CDFW) at the LAR Nimbus Hatchery from 2008 to 2011 [64]. The egg-fry survival rate (EF) was set to 0.67 based on a Chinook Salmon egg survival study conducted on the LAR [64]. These constants were used to estimate the total number of emerging fry. Additionally, a proportion of each cohort (30%) was designated as non-natal rearing, a common Chinook Salmon emigration behavior [134, 106, 2]. However, a likely driver of early emigration is lack of natal rearing habitat [2], and there is evidence that this behavior results in reduced survival compared to juveniles that rear in-river before Delta entrance [101, Sturrock et al., *in press]*. Therefore, we set the non-natal rearing proportion lower than is currently observed to allow us to explore the effects of increasing habitat extent on in-river rearing capacity.

Juvenile emigration timing, mode, and rate are influenced by multiple environmental and biological cues [120, 134]. Although Chinook Salmon emerge from redds as fry, they do not all begin downstream emigration immediately. Fry emigration initiation may indicate that the local juvenile carrying capacity is being reached [87]. Alternatively, fry emigration may be maintained as an advantageous life-history strategy during drought years when Delta water quality degrades early in the rearing period and late migrant survival is likely to be low [68, Sturrock et al. *in revision]*. Instead of attempting to model the complex mechanisms that trigger emigration, we applied the average behavior of LAR emigrants observed during sampling in previous years to have juveniles commence emigration at the time and size appropriate for the LAR.

3.1.3 Growth and Survival

Daily system-specific survival and growth rates are applied to all cohorts in the system prior to any behavioral or spatial updates [28, 109]. Next, habitat occupancy (territory size, see below) and maximum daily migratory distance calculations are applied, updating these metrics for each cohort, both of which are functions of fork length [10, 41]. Cohorts exceeding a 100 mm fork length transition to the *Migrating* behavioral state [30].

Each day, if cohorts were present in the system, they experience survival rates according to their current behavior. Under default conditions, survival was set to a daily rate of 0.96, independent of behavior [28]; however, we explored impacts from varying this parameter according to behavior (rearing or migrating; described below). Modeled salmon also grow daily, with growth rates dependent on their location. Specifically, salmon located upstream of RKM 15 grow faster than those downstream at a rate of 0.52 +/- 0.1 mm/day compared to 0.47 +/- 0.1 mm/day [109]. If any cohorts exceed the maximum rearing size threshold of 100 mm, they switch to behavioral state *Migrating* and begin emigration [30, Water Forum, unpublished data]. After the new fork length of the cohort is calculated, the total area that the cohort occupies is updated using the territory size equation from Grant and Kramer (1990).

Territory size determines the amount of habitat that each cohort occupies. Territory size is modeled as a function of fish fork length (Eq. 2), informed by a meta-analysis of territory size versus fish size relationships for various salmonid species [41] (Eq. 2; Fig. 5).

Territory size for individual fish = $10^{-5.44+2.61\log_{10}(fork\ length)}$ (2)

Recent studies [52], despite lacking observations at maximum fish densities, report minimum territory sizes consistent with the prediction intervals of the Grant and Kramer (1990) model, supporting its robustness. In the model, territory size for an individual fish is estimated based on its fork length and then scaled by cohort size (number of fish in the cohort) to determine total habitat requirements for the cohort.

The cohort's maximum daily migratory distance was calculated based on the fork length of the fish in the cohort. This distance is a function of 0.04 RKM/day multiplied by the fork length [10]. Cohorts that are actively migrating travel this full distance each day. Cohorts searching for rearing habitat may stop

before reaching the maximum distance if suitable available habitat is found. Otherwise, they continue to migrate until the daily migratory limit is reached.

3.1.5 Natal Rearing Behavior and Habitat Occupancy

The habitat occupancy distribution is populated starting with fry emergence. In the model, cohort behavioral states are influenced by river location, available habitat, and cohort fork length. Fork length plays a critical role, as larger individuals are more capable of defending territories, giving them priority access to habitats over smaller individuals [130].

Moving sequentially downstream, behavioral states are updated based on habitat occupancy. If the current reach exceeds capacity, the cohorts with the smallest fork length and behavior state *Rearing* transition to *Looking*, until the reach is at capacity. Conversely, if a reach is under capacity, cohorts attempting to establish rearing territory are reassigned from *Looking* to *Rearing*, prioritizing cohorts with larger fork lengths. Cohorts are subdivided as needed to match available habitat or to reach capacity.

Following behavioral updates, cohorts move according to their assigned behavior. *Rearing* cohorts remain in place, while *Migrating* cohorts emigrate according to their size-dependent maximum daily migratory distance. Note: *Migrating* cohorts only move once per day, always at their maximum distance. Once their daily distance is complete, they do not emigrate farther until the following day. *Looking* cohorts move to the next RKM, searching for available rearing space until suitable habitat is found or the maximum daily distance is reached.

At the end of each day, cohorts located downstream of RKM 0 are considered emigrants and are removed from the simulation. This daily sequence is repeated until the end of July, when all cohorts have emigrated from the system.

Table 1

Model parameters, units, values, and data sources used in the Lower American River (LAR) Emigrating Salmonid Habitat Estimator (EHSE) model for salmon entry and behavior. Values are based on field data, published literature, and modeling assumptions. See details on parameter values and sources in the following sections.

	Parameter (units)	Value(s)	Data Source(s)
Model Entry	Returning Adults (number of fish)	22,930	15-year (2009–2023) average of in-river LAR adult returns [3]. This assumes a 1:1 sex ratio and that females have a fecundity of 6,001 eggs [98]. Eggs have a survival rate of 0.67 [66].
	Location (proportion of fry per km)	various	Percent of redds observed by RKM from 2012 through 2023 aerial LAR surveys [USBR, unpublished data, 2012–2021, 107].
	Timing (daily proportion of fry)	various	Temporal spawning distribution estimated from 2023 LAR spawning ground survey data, applying a truncated normal distribution to smooth the raw data [108]. Emergence timing was estimated by calculating 750 degree-days from the spawning date [75, 6].
	Size (mm)	36	Initial salmon size when they emerge from the gravel [30].
Behavior	Survival (per day)	0.96	Daily survival rate [28].
	Growth (mm/day)	Upper River: 0.52 Lower River: 0.47	Daily growth rates from 2021–2024 LAR passive integrated transponders mark-recapture study [109].
	Migration Rate (rkm/day)	0.04 * fork length	Migration rate is multiplied by fish size to determine the maximum distance salmon can migrate per day [10].
	Habitat Required (m^2)	$10^{-5.44+2.61\log_{10}(forklength)}$	Relationship between salmon territory size (m^2) and fork length (mm) for multiple salmonid species [41]

3.2 Model Output and Application Scenarios

The model outputs daily information for each cohort within the system, highlighting the spatial and temporal distribution of the cohorts. This includes the number of fish per cohort, their behavior, river location, territory occupied at the cohort-level and individual-level, migration distance, day of emergence, and number of days in the system. In addition to daily results within the system, the model outputs

cohort-level data upon emigration from the system, including the number of days spent in the river, the cohort size, and individual fish size.

The ESHE model provides a quantitative tool to inform habitat restoration planning and support long-term habitat maintenance and population recovery. We developed five scenarios to demonstrate potential applications of the LAR ESHE model for management decision-making (Table 2). For all scenarios, a daily survival rate of 0.96 and an emigration size threshold of 100 mm were applied.

Table 2
Model inputs and outputs used to evaluate management scenarios in the LAR using the ESHE model. Scenarios vary in habitat availability, flow conditions, returning adult abundances, and non-natal rearing assumptions, with outputs including habitat deficits and maximum habitat utilization.

Scenario	Model Capacity	Comparison Flow	Returning Adults	% non-natal rearing	Output
1. Variation in habitat deficit under different flow conditions with the present population	Maximum potential habitat for 21, 71, and 425 m^3/s flows	Present available habitat for 21, 71, and 425 m^3/s	22,930	30	Habitat deficit by RKM for high, medium, and low flows
2. Variation in habitat deficit under three flow conditions with the goal population	Maximum potential habitat for 21, 71, and 425 m^3/s flows	Present available habitat for 21, 71, and 425 m^3/s	160,000	30	Habitat deficit by RKM for high, medium, and low flows
3. Compare habitat needed in February and April under spring base flow (drought) conditions	Maximum potential habitat for 21, 71, and 425 m^3/s flows	Present available habitat for 21, 71, and 425 m^3/s	160,000	30	Habitat deficit by RKM for low flow during February and April
4. Habitat needed to support the present population	Infinite m^3/s RKM	N/A	22,930	0-100	Maximum habitat for each non-natal rearing percentage
5. Habitat needed to support the goal population	Infinite m^3/s per RKM	N/A	160,000	0-100	Maximum habitat for each non-natal rearing percentage

The first scenario examines how current population habitat deficits along the river corridor vary under low, medium, and high flow conditions. The model is run once for each flow level. To simulate this scenario, the available habitat for every RKM is set to the maximum potential habitat for a given flow level. The number of returning adults is set to the current adult return population (Table 1), while all other

model inputs remain at their default values. The simulation tracks daily habitat use per day, per RKM, which is used to calculate the maximum habitat utilized at each kilometer over the entire simulation. The habitat deficit is calculated as the difference between the maximum territory used from model output and the present available habitat for each RKM. The second scenario follows the same procedure as the first, using the goal population.

The third scenario explores how habitat requirements vary throughout the rearing period under drought conditions (low flow), comparing habitat demand at rearing season initiation (February) to later (April) under the goal population. Low flow was chosen because flow pulses are a common management tool hypothesized to ameliorate drought effects on juvenile salmonids; therefore, understanding when this action would be most useful would help inform management action timing. To simulate this scenario, the maximum potential habitat for low flow and the goal population were used. All other inputs remained at default values. The simulation recorded daily habitat use per RKM, which was used to calculate the maximum habitat used for each RKM for each day in February and each day in April. Present, available habitat under drought conditions was then compared to the maximum habitat from ESHE output to find the habitat deficit by RKM for each month.

The fourth scenario estimates the effect of non-natal rearing behavior on the total habitat required across all RKMs to support juveniles produced under the current returning adult population. This scenario examines model outcomes across a range of proportions of non-natal rearing fish, from 0% to 100% in 10% increments, to assess how maximum habitat requirements vary with the prevalence of this migratory strategy. Prior to model run, the available habitat for every RKM was set to infinity, allowing juveniles to rear freely without spatial limitations and preventing habitat from influencing modeled fish behavior. Each day, the model calculates the total habitat used, defined as the summed area of rearing habitat occupied by all fish across the system. The day with the highest summed area represents the maximum habitat requirement for that proportion of non-natal rearing fish.

The fifth scenario applies the same approach as scenario four, using the goal population to estimate the maximum habitat requirements under the management target across the same range of non-natal rearing proportions.

In addition to these five scenarios, we demonstrated a potential application of the ESHE model to support habitat restoration planning: identifying river reaches with the greatest habitat deficits under varying flow and population conditions. This exercise provides outputs that predict additional growth and behavioral metrics, including the seasonal timing of peak habitat deficit, fish size at that time, rearing duration, and the mean size of emigrating fish across different flow and population scenarios.

3.3 Sensitivity Analysis

A one-at-a-time sensitivity analysis was performed on the ESHE model to assess its performance and evaluate how uncertainty in parameter estimates affects model outputs. The four parameters tested included migration and rearing survival rate, migration rate, and available habitat. Starting from each

parameter's default value, values were adjusted by ± 1%, ± 5%, ± 10%, ± 20%, and ± 30%, with an upper bound of 1 applied to survival rates. The analysis used the current adult population under low-flow conditions, while all other parameters remained at default settings. For each adjusted value, the model was rerun with all other parameters held constant. Outputs were measured as total habitat used on the day of peak occupancy for each simulation, and results were compared to the baseline to calculate change in maximum habitat use for each parameter.

4. Results

For Scenario 1, most RKM reaches exhibit a small to moderate habitat deficit

(≤ 0.1 km²), with deficits distributed relatively evenly across the three modeled flow conditions (Fig. 6). The largest deficits occur in the upstream river section, between RKMs 25 and 36—the primary spawning reach where most fry emerge and enter the model. At all flow levels, RKMs 13, 14, and 17 provide sufficient habitat to support juveniles produced by the current population. Notably, RKM 25 exhibits a much larger deficit under low-flow conditions compared to medium or high flows. Overall, this scenario closely reflects the spatial distribution of spawning.

Scenario 2 resulted in all RKMs exhibiting habitat deficits regardless of flow level under the present habitat availability (Fig. 7). Across most reaches, deficits were relatively uniform for the three flows, and the distribution does not resemble the spawning distribution.

Scenario 3 demonstrates the habitat deficit for the goal population under drought conditions earlier in the rearing season compared to later (Fig. 8). In February, every RKM had a larger habitat deficit compared to April, when fewer juveniles are rearing in the LAR. The greatest deficits during both February and April occurred between RKMs 13 and 21, with the exception of RKM 18.

The fourth and fifth modeled scenarios demonstrate that as the portion of non-natal rearing juveniles increases, the LAR habitat required to support juveniles decreases (Fig. 9). When we adjusted the model to have 100% natal rearing, the maximum rearing habitat required was 1.43 $km^{2,}$ and shifted to 0.71 km^2 when 100% were non-natal rearing, for the current population. A similar pattern occurs under scenario 5 for the goal population (Fig. 9b). The resulting maximum habitat requirement was 9.95 km^2 when 100% were natal rearing and decreased to 4.92 km^2 when 100% were non-natal rearing (Fig. 9b).

We used the ESHE model to generate predictions of when and where the greatest habitat deficit would occur under low, medium, and high flow scenarios and under the current and goal population sizes (Table 3). In all cases, the day with the greatest over-capacity occurred between the 17th and 22nd of February. The mean fork length of fish rearing in the LAR (i.e., *Rearing* and *Looking* fish) and of all fish in the system on the day of greatest habitat deficit was slightly smaller under the current returning adult population compared to the doubling goal. The RKM reaches with the highest habitat deficit differed somewhat depending on flow and population size, with RKM 20 noted in all six cases, RKM 21 in five of the six cases, RKM 16 in four of the six cases, and RKM 13 and 14 in three of the six cases. Returning

adult population size (current or doubling goal) had a strong effect on both the mean fork length of all emigrating fish and the mean total number of rearing days before emigration. For both population sizes, both metrics were highest under high flow conditions and similar under low and medium flows.

Table 3
Summary of rearing juvenile Chinook Salmon behaviors, habitat use, and river deficits for the current population (22,930 returning adults) and goal population (160,000 returning adults) deficit under low (21 m^3/s), medium (71 m^3/s), and high (425 m^3/s) flow conditions.

Metric/flow	Current population			Goal Population		
	Low	Medium	High	Low	Medium	High
Date with maximum over capacity	19 February	17 February	22 February	19 February	18 February	17 February
Mean rearing Chinook Salmon fork length (mm)	52	52	53	54	54	53
Mean fork length of all rearing Chinook Salmon in the LAR on the date of maximum habitat deficit	50	50	51	51	51	51
Five LAR RKMs with the greatest habitat deficit	14, 20, 19, 17, 13	21, 20, 14, 19, 16	10, 15, 21, 16, 20	10, 16, 13, 20, 21	16, 20, 21, 12, 15	13, 9, 20, 21, 14
Mean Chinook Salmon fork length at emigration time	63	63	66	57	57	58
Mean days in the system before emigrating	56	54	61	43	43	46

Sensitivity analysis revealed that the ESHE model results were most sensitive to migration survival rate, followed by rearing survival rate, migration rate, and available habitat (Fig. 10). Sensitivity was evaluated as the change in the maximum habitat used relative to the baseline output, where delta was 0. Variables that produced larger deviations from the baseline prediction were considered more influential on model outcomes than those that produced smaller changes.

5. Discussion

Estimating habitat deficit is critical for managing migratory species because it can reveal where and when resource limitations occur along migration pathways. Unlike resident species, migratory populations rely on a network of connected habitats, at any one life stage can propagate through the life cycle, constraining population performance [124]. For example, modest loses of intertidal habitat in the East Asian–Australasian Flyway have been shown to cause disproportionately large declines in

migratory shorebird populations [51]. The ESHE model addresses this challenge by providing a river-specific, spatiotemporally explicit framework for estimating juvenile rearing habitat requirements under varying flow and population conditions. Applied to the LAR system, ESHE quantifies the amount and distribution of habitat needed to support both current and CVPIA target populations across the rearing season, while also identifying key data gaps through sensitivity analysis. By explicitly linking habitat availability to population objectives, habitat deficit estimates from ESHE can support targeted restoration, help prevent bottlenecks, and inform strategic, large-scale conservation planning [4, 118].

5.1 Spatial Distribution of Habitat Deficit

Our model indicated that habitat deficit varied strongly with population size. Under the current population, deficits were greatest in upper LAR reaches where spawning occurs, reflecting the concentration of fry emergence and high localized demand for rearing space. Under the management doubling goal, capacity was exceeded across a broader corridor as juveniles dispersed downstream in search of available habitat. These patterns reflect interactions among juvenile abundance, rearing behavior (natal vs. non-natal), and habitat availability, with higher densities intensifying competition and density-dependent constraints on growth and survival [110]. Consistent with size-structured habitat use, larger fish secure space first, pushing smaller fish downstream as reaches fill, further concentrating demand in downstream sections. In a simplified system such as the LAR, habitat availability and spawning-reach use by emerging fry appear to be dominant drivers of spatial habitat deficit [2, 5, 102, 9]. The spatiotemporal distribution of deficits will shift with restoration, as actions alter habitat extent and capacity and thereby influence growth and survival; because restoration in regulated rivers is transient and habitat features degrade through altered flow, sediment supply, and spawner disturbance [22, 63, 53, 66], ESHE outputs should be updated iteratively as habitats evolve, projects are implemented, and new data become available.

5.2 Effect of Flow on Habitat Deficit

We observed minimal variation in rearing habitat deficits across modeled flow conditions within individual reaches. This pattern is consistent with other impounded rivers, where channel incision and floodplain disconnect limit seasonally inundated rearing habitat, confining suitable depths and velocities to narrow channel margins rather than expansive floodplains or side channels [53, 72, 19].

In the LAR application, limited flow-related variation in available habitat within restored reaches (RKM 36–21) also reflects the restoration design approach. Projects are typically engineered to provide stable rearing habitat across a targeted range of managed flows shaped by reservoir operations, which dampen winter and spring variability relative to historical conditions [133, 18]. By integrating predicted habitat outputs from proposed designs, ESHE enables managers to evaluate population-level responses to alternative flow regimes prior to implementation, supporting more strategic and cost-effective restoration planning.

5.3 Seasonal Differences in Habitat Deficit

Estimating habitat extent across flow conditions is necessary to inform ecologically effective flow management, but habitat metrics alone are insufficient for guiding restoration or operational decisions. Their management relevance depends on understanding juvenile behavior, specifically when and where fish are present, how many are rearing versus emigrating, and how these behaviors change through the season. By explicitly incorporating emergence and emigration dynamics, ESHE moves beyond static habitat quantification to predict when habitat limitation is most biologically consequential. Results from Scenario 3 demonstrate that habitat deficits are greatest early in the rearing period, when fry emerge from gravel and compete for rearing space, a phase that typically coincides with peak juvenile densities and heightened sensitivity to habitat availability [46, 42, 87]. As the season progresses, habitat limitation diminishes as juveniles emigrate or experience mortality, reducing in-river density by April. These patterns suggest that, under current LAR conditions, restoration and flow management actions that increase shallow, low-velocity habitat during winter and early spring (February–March) are likely to yield the greatest ecological benefit. In particular, under low-flow conditions where spring flow pulses are used to support juvenile rearing, earlier implementation may be more effective because it aligns with the period of greatest habitat constraint and allows a larger fraction of the population to benefit.

5.4 Relationship Between Habitat Deficit and Emigration Strategy

Our model showed that life-history composition strongly mediates habitat demand: the prevalence of natal versus non-natal emigration varies with habitat capacity, density, and hydrology, shaping size at ocean entry and survival [2, 106, 49]. Within ESHE's size- and density-structured allocation, larger fish secure space first, pushing smaller fish downstream as reaches fill, which shifts where and when habitat deficits materialize [2, 106, 49]. System-wide habitat need halved as the non-natal proportion increased from 0% to 100%, demonstrating that the natal vs. non-natal mix strongly influences restoration demand. For planning, reach-level targets should be evaluated across plausible ranges of life-history composition and seasonal demand, rather than a single fixed value [2, 106].

While ESHE focuses on the natal rearing component of the life cycle, future extensions could incorporate survival through the migratory corridor (e.g., the Delta and Pacific Ocean) to evaluate how restoration and emigration strategies influence survival to adulthood.

5.5 Predicting Locations of Habitat Deficit and Biological Metrics

Our results suggest that ESHE outputs can be used to prioritize reaches where habitat is limiting across flow and population scenarios. By linking habitat availability to predicted growth, behavior, and residence time, the model also provides a mechanism for aligning flow management and restoration timing with periods when juvenile salmon are most sensitive to habitat constraints. Model results further suggest that increasing juvenile abundance leads to reduced mean emigrant size and earlier emigration, reflecting density-dependent trade-offs between in-river production and downstream survival [110]. This pattern is consistent with a broad body of literature demonstrating that smaller juvenile salmon generally

experience lower survival to adulthood, particularly during early migration and marine entry. Consequently, actions that increase juvenile production without a commensurate increase in rearing habitat may inadvertently reduce cohort-level survival [94, 123]. These dynamics have direct implications for in-river hatchery and supplementation practices, as large or poorly timed releases can increase local densities, displace natural-origin juveniles, and promote earlier emigration at smaller sizes [14, 54]. Finally, restoration and flow-management actions informed by ESHE outputs should be evaluated alongside project costs, land-ownership constraints, cultural values, and stakeholder priorities to ensure that restoration strategies are both biologically effective and feasible within highly managed river systems [8, 80].

5.6 Sensitivity Analysis

Sensitivity analyses clarify which uncertainties most affect predictions and, therefore, where to focus monitoring and model refinement [23, 132]. In ESHE, outputs were most sensitive to migration and rearing survival, and less sensitive to migration rate and available habitat as adjusted here. Because current survival estimates are derived largely from a single hatchery-based study and hatchery fish can behave differently from natural-origin fish [39, 79, 99], we recommend two management/readiness actions:

(1) Treat absolute habitat-area estimates cautiously until behavior-specific survival (rearing vs. migrating) is refined; in the near term, emphasize relative reach-ranking and timing outputs for decision support.

(2) Prioritize new research on natural-origin, behavior-stratified LAR survival (e.g., estimating daily survival separately for natal-rearing and non-natal migrants) to reduce the dominant source of model uncertainty and improve the reliability of habitat targets.

5.7 Management Implications

The ESHE model provides a decision-support framework that translates population objectives into explicit estimates of where, when, and how much juvenile rearing habitat is required in a regulated river. By linking habitat availability with size- and density-dependent behavior, ESHE enables managers to move beyond static habitat metrics toward evaluations that account for fish distribution, timing, and capacity constraints. This approach supports restoration planning that prioritizes biologically meaningful actions while balancing feasibility and uncertainty.

Spatial prioritization is a central application of ESHE. The model identifies river kilometers that consistently experience habitat deficits across flow conditions and population sizes, highlighting reaches where limited rearing capacity is most likely to constrain juvenile production. Reaches that rank highly under both current and goal-population scenarios represent robust restoration candidates because they are likely to remain limiting as abundance or operations change. These spatial rankings can be integrated with practical constraints such as cost, land ownership, and infrastructure to guide selection of implementable projects [8, 80].

ESHE also informs seasonal timing of management actions. By simulating emergence, rearing, and emigration on a daily timestep, the model identifies periods when habitat limitation is most acute. In this application, the greatest constraints occurred early in the rearing season (February), when juvenile densities peak and competition for shallow, low-velocity habitat is strongest. Restoration or flow actions that increase nearshore habitat area and complexity during this early window are therefore expected to yield greater biological benefits than actions implemented later in spring [122, 7].

Planning under uncertainty is facilitated by ESHE's ability to evaluate habitat demand across alternative life-history compositions. Modeled habitat requirements vary with the prevalence of natal versus non-natal emigration strategies, with higher proportions of non-natal emigrants reducing system-wide rearing demand. Because life-history composition can shift with density and hydrology, managers should evaluate ranges of habitat need across plausible emigration scenarios and emphasize relative reach ranking and timing, which are more robust to parameter uncertainty than absolute habitat values [89].

In regulated rivers, restoration benefits are often transient due to altered sediment supply, channel simplification, and repeated disturbance, necessitating periodic reassessment and maintenance [53, 22, 18, 66]. ESHE can be rerun as habitat conditions evolve to update reach priorities and inform long-term maintenance planning [80].

Although ESHE focuses on freshwater rearing, outputs can be combined with assumed downstream and marine survival to estimate the natal-stream habitat contribution required to meet adult return targets [84, 85]. Presenting habitat requirements as ranges under alternative post-emigration survival scenarios clarifies the role of in-river restoration within basin-scale recovery strategies [118].

Used iteratively, ESHE aligns restoration location, timing, and scale with population objectives while explicitly incorporating uncertainty and feasibility, supporting adaptive and cost-effective recovery planning.

Declarations

Ethics Approval

Not applicable, as this manuscript is based on a life cycle modeling framework.

Consent to Participate

Not applicable, as this manuscript is based on a life cycle modeling framework.

Consent to Publish

Not applicable, as this manuscript is based on a life cycle modeling framework.

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contribution

Model conceptual and framework, along with biological input, were provided by Joseph Merz. Biological data collection and biological input were provided by Kirsten Sellheim. Physical habitat modeling was provided by Pete Moniz. Model coding and shiny application creation was completed by Kiera McNeely and Kai Ross. All authors contributed to the manuscript.

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Data Availability

An interactive implementation of the model is available as a Shiny application at:https://fishsciences.shinyapps.io/AllFlowsESHE Some recent data used to generate this model is available online at the links listed below. Other datasets were taken from various publications, which are listed in Table 1. The code used to generate the model is available from the authors upon request.Habitat suitability quantification: https://waterforum.org/wp-content/uploads/LAR_2023_Habitat_Quantification_TM_2024-12-18_wFigures.pdf Returning adults: https://wildlife.ca.gov/Conservation/Fishes/Chinook-Salmon/Anadromous-AssessmentRedd location (aerial survey data) and migration speed: Technical reports available by request from the authors or Sacramento Water Forum.Redd timing: https://doi.org/10.6073/pasta/1e5b04181efe3f1c745f1c45af535c72Growth rates: https://doi.org/10.6073/pasta/94593d989cf600a626fe826f2340e024

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Figures

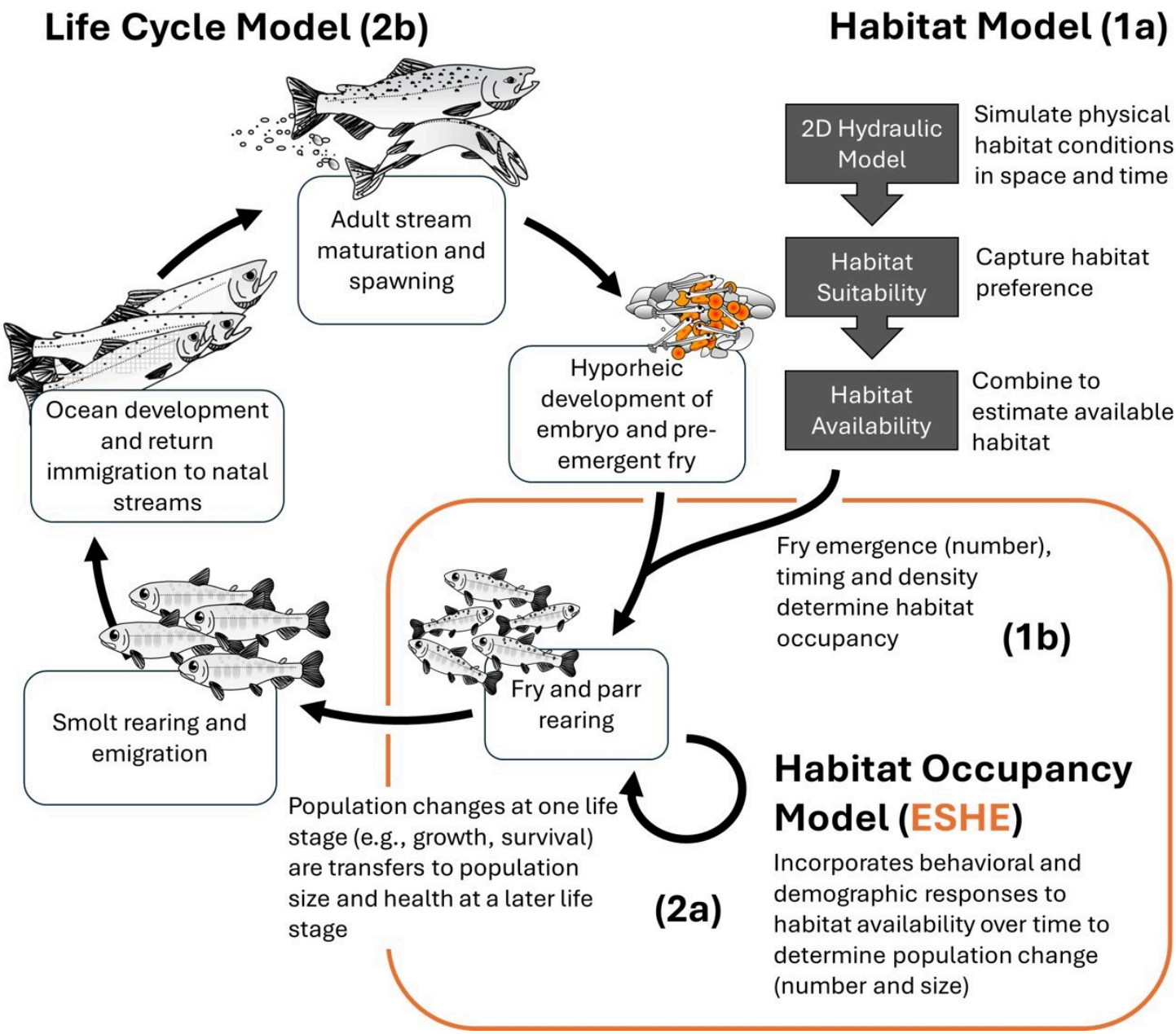


Figure 1

Conceptual framework linking habitat conditions to the generalized Central Valley Chinook Salmon life cycle. The life cycle (2b) includes key life stage transitions from adult spawning through juvenile rearing and emigration to adult escapement. The habitat model (1a) depicts habitat availability across space and a range of flows. The habitat occupancy model (1b) links the habitat model to the life cycle model by describing habitat use by the concurrent population over time and predicting life stage-specific changes (e.g., growth, movement, survival) that inform subsequent life stage size and condition.

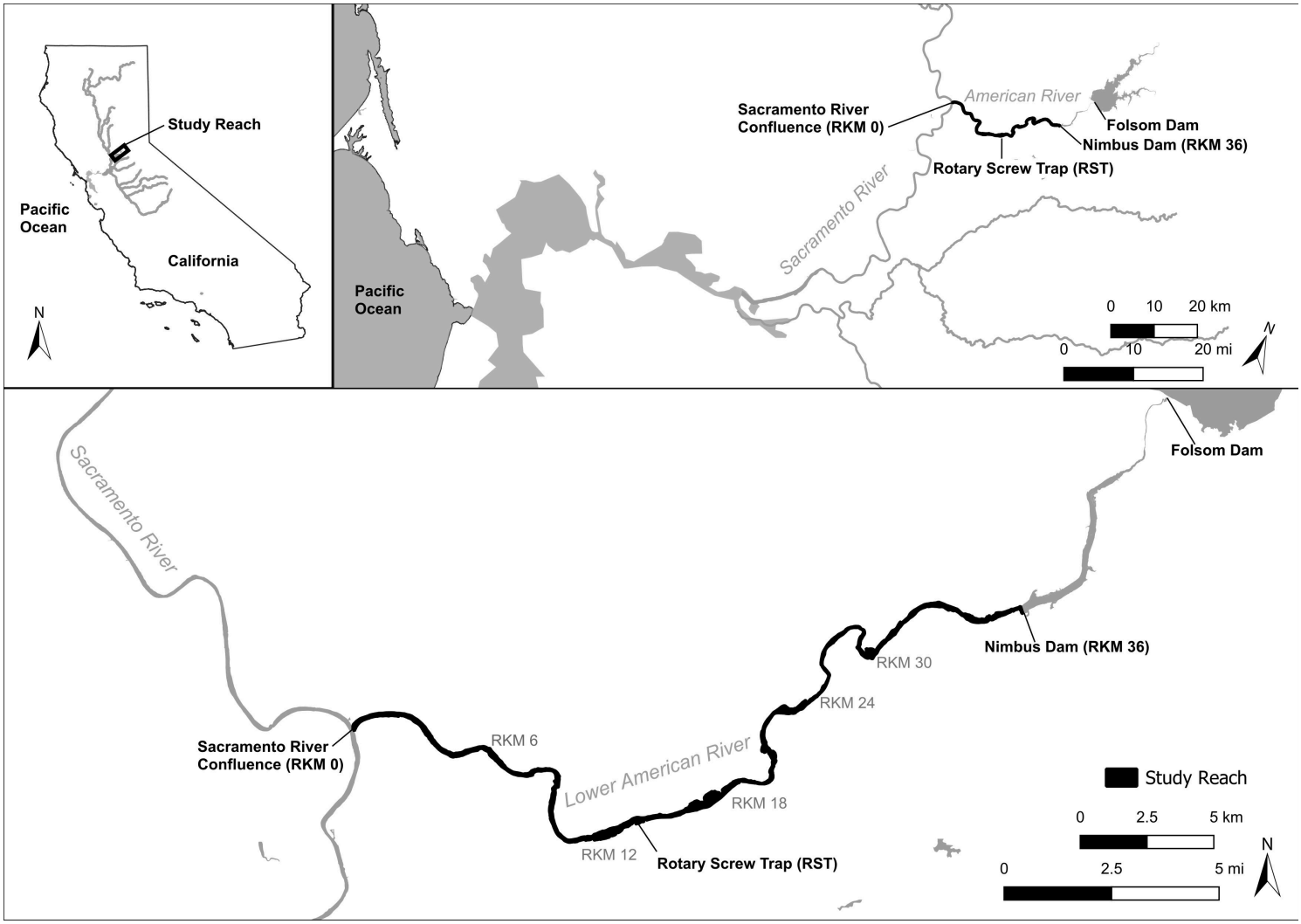


Figure 2

Maps showing the study reach of the Lower American River (LAR), including the location within the California Central Valley (top left), the LAR's path to the Pacific Ocean (top right), and a detailed view of the LAR (bottom panel). The LAR Emigrating Salmon Habitat Estimator model spans from Nimbus Dam (RKM 36) to the Sacramento River confluence (RMK 0), with key river landmarks shown.

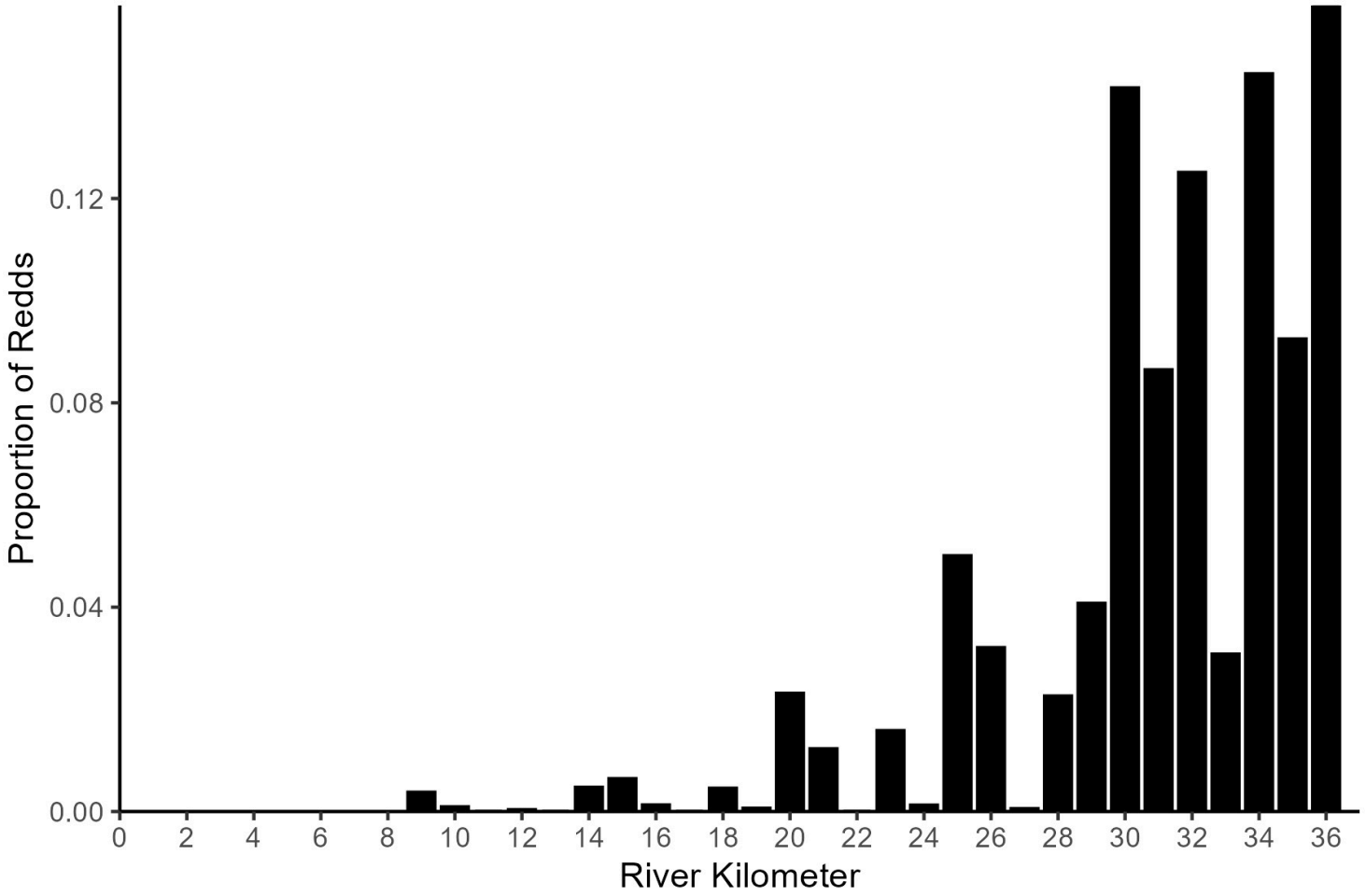


Figure 3

Average proportion of fall-run Chinook Salmon redds observed by river kilometer in the Lower American River, based on annual redd survey data collected from 2012 to 2023, illustrating the spatial distribution of spawning along the river [107, Reclamation unpublished data].

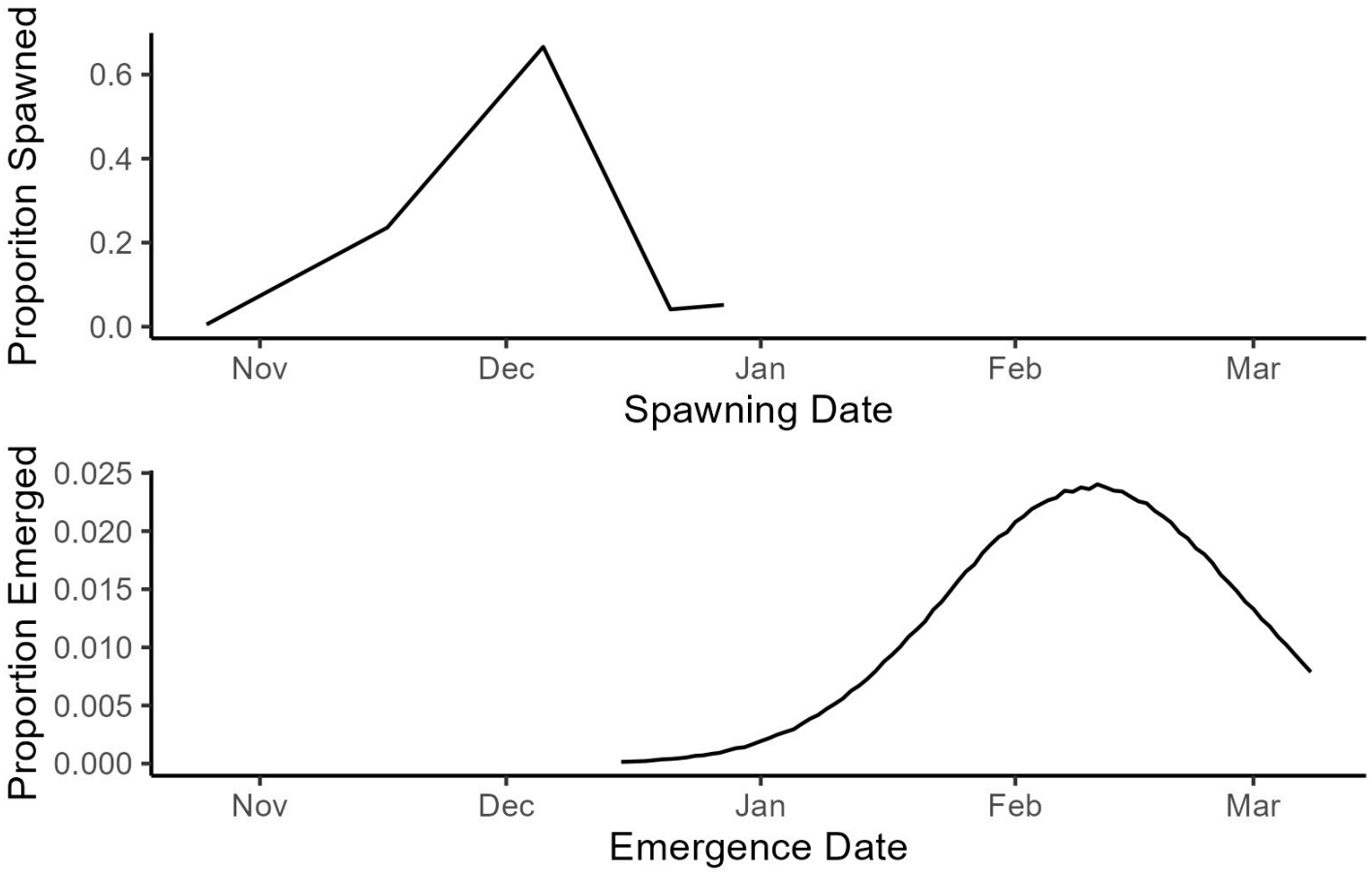


Figure 4

Raw temporal distribution of fall-run Chinook Salmon redds in the Lower American River from 2023 surveys [108] (top panel) and the corresponding smoothed truncated normal distribution used to predict fry emergence timing (bottom panel). Emergence was estimated using the daily water temperatures and 750 degree-days. The relative emergence dates and proportions were used to initiate the Emigration Salmonid Habitat Estimator model.

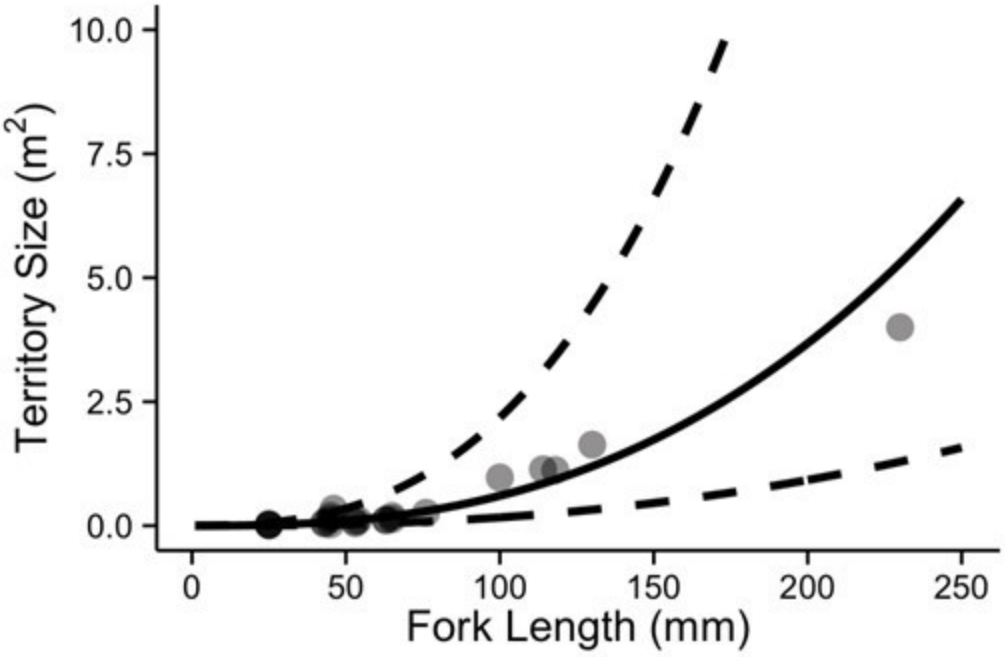


Figure 5

Relationship between salmon territory size and fork length. Points represent individual fish observations, the solid line shows the mean relationship, and dashed lines represent the upper and lower 95% prediction interval limits. Adapted from Grant and Kramer (1990).

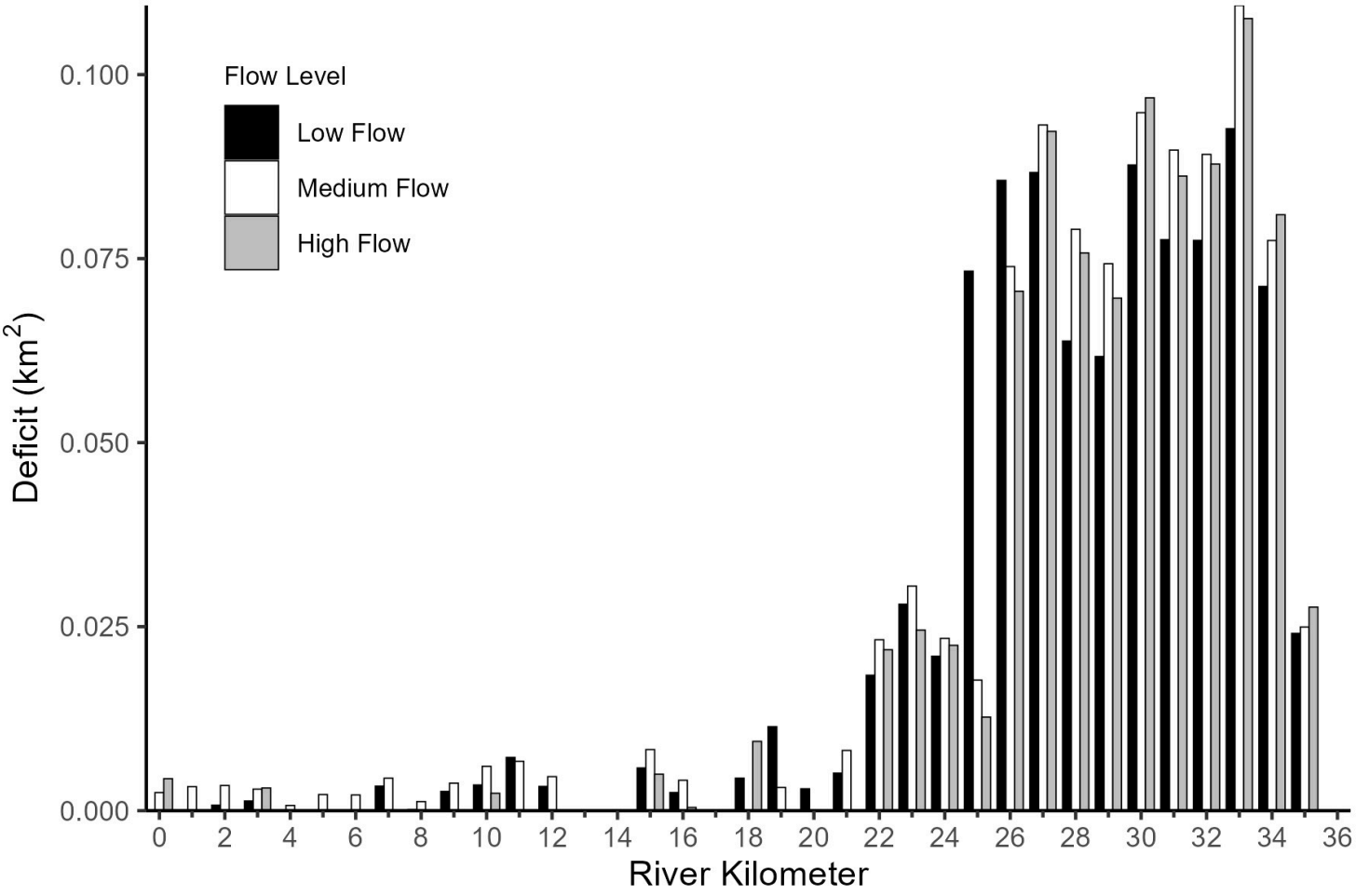


Figure 6

Habitat deficit per river kilometer (RKM) for the current adult population (22,930 returning adults) under low (21 m³/s), medium (71 m³/s), and high (425 m³/s) flow conditions. The deficit is the difference between the maximum habitat occupied per RKM when the Emigration Salmonid Habitat Estimator uses the maximum potential habitat, and the present habitat available for a given flow.

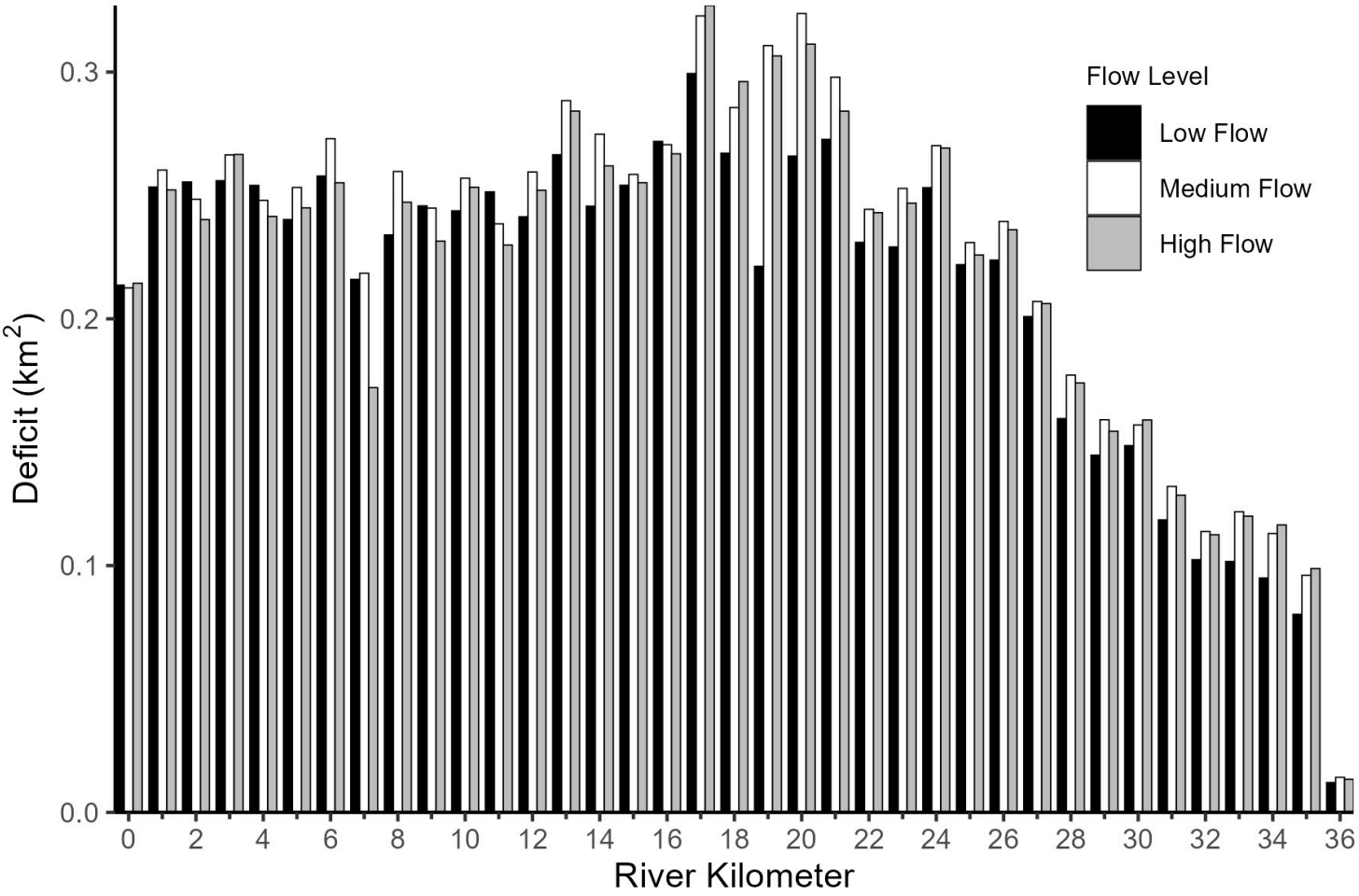


Figure 7

Habitat deficit per river kilometer (RKM) for the goal population (160,000 returning adults) under low (21 m³/s), medium (71 m³/s), and high (425 m³/s) flow conditions. The deficit is the difference between the maximum habitat occupied per RKM when the Emigration Salmonid Habitat Estimator uses the maximum potential habitat, and the present habitat available for a given flow.

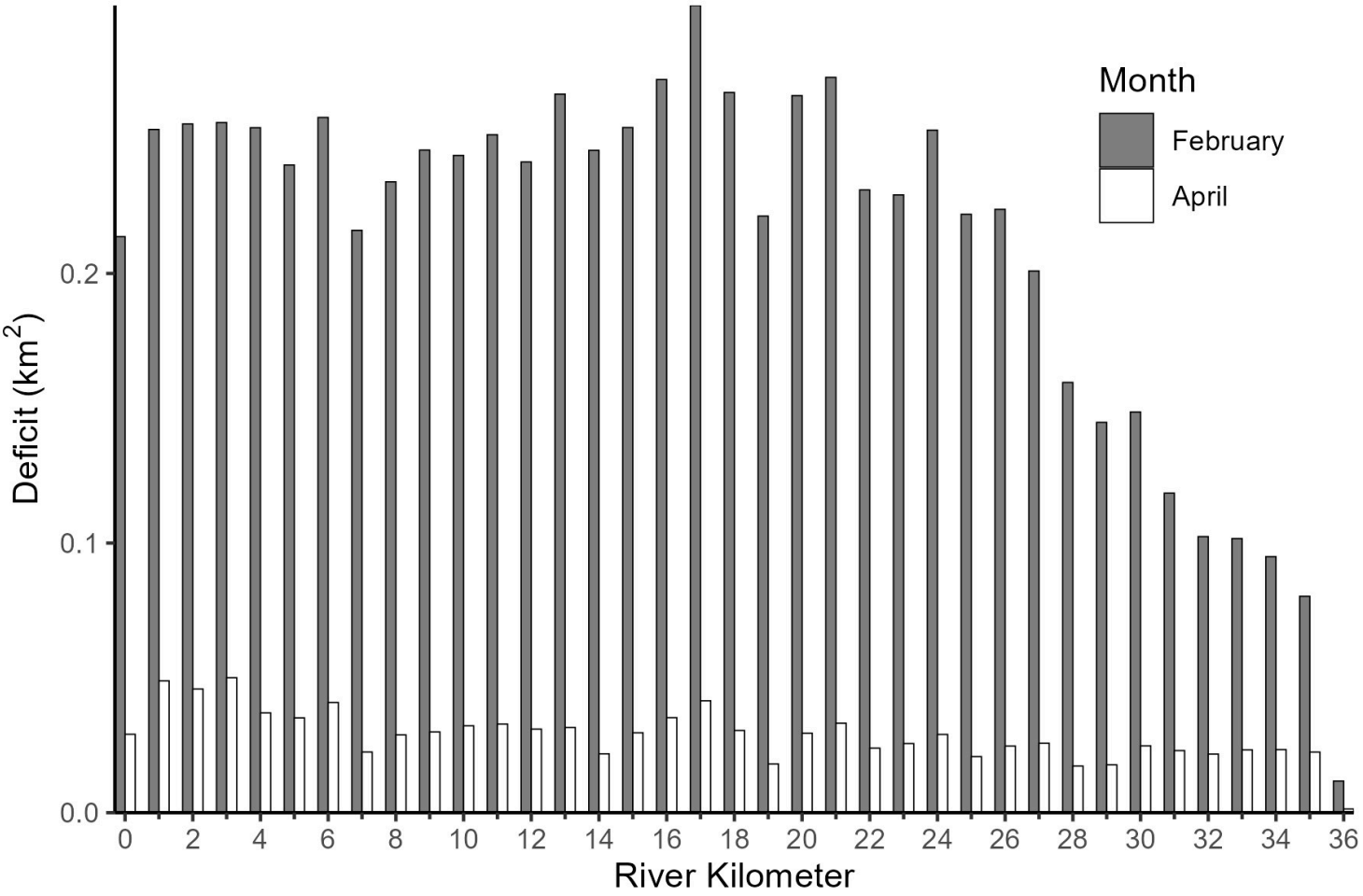


Figure 8

Habitat deficit per river kilometer (RKM) under the goal population (160,000 returning adults) in February and April at base flow (21.34 m^3/s), representing a spring drought year. The deficit was calculated by running the Emigrating Salmonid Habitat Estimator model with the maximum potential habitat at base flow, calculating the maximum habitat occupied per RKM for each month, and comparing it to the present available habitat. Absence of bars indicates no deficit.

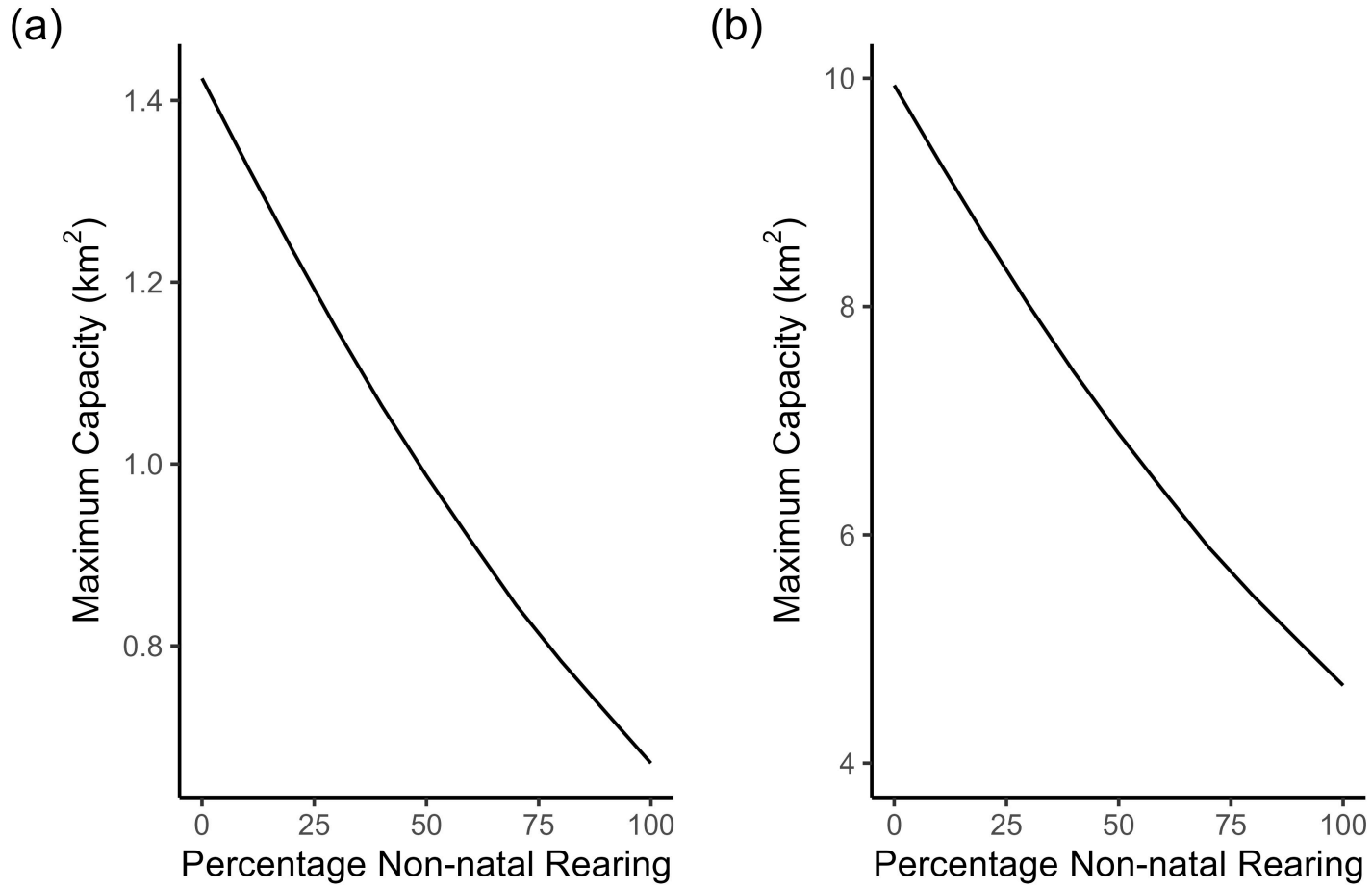


Figure 9

Estimated maximum habitat required to support juveniles across all river kilometers (RKM) under varying proportions of non-natal rearing fish. Panel (a) shows the current returning adult population (22,930 adults), and panel (b) shows the goal population (160,000 returning adults). The ESHE model was run with infinite kilometers squared for each RKM to isolate the effect of non-natal rearing behavior on habitat use. Maximum capacity was calculated as the highest total territory occupied in the model for each proportion of non-natal rearing juveniles. Note that the Y-axis range differs between the two panels.

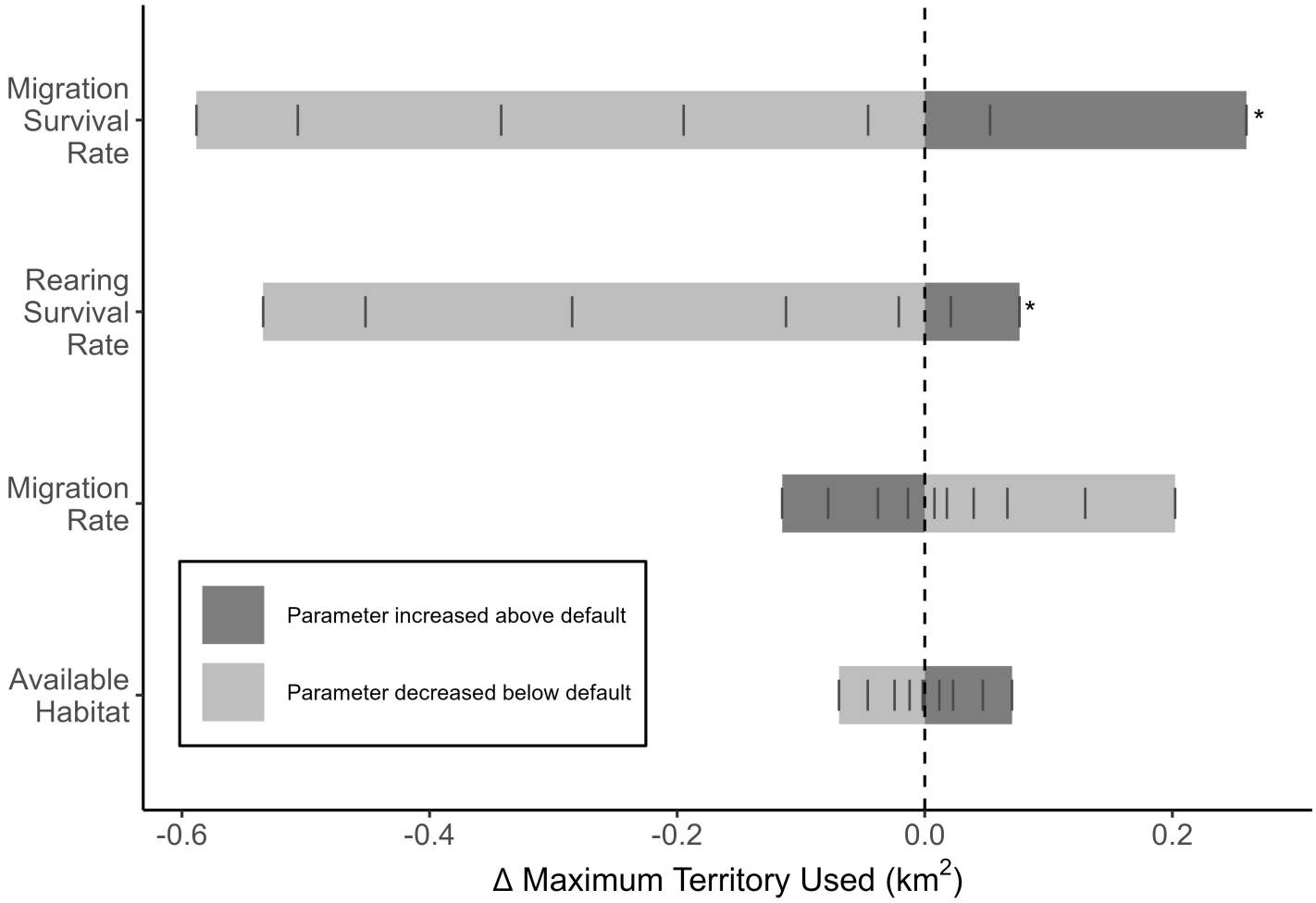


Figure 10

One-at-a-time sensitivity analysis showing how changes in individual model inputs affect the predicted maximum habitat used in a simulation day, ordered from most to least sensitive. Tick marks denote the output from each input value, with asterisks (*) indicating that the input exceeded the biological limit for that parameter, causing the model output to reach its maximum or minimum value, producing identical results across multiple runs. Bar colors indicate whether the input value was increased or decreased relative to the default model value.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Table1.jpeg
- Table2.jpeg
- Table3.jpeg