`APPLICATION OF A SALMONID LIFE CYCLE MODEL FOR EVALUATION OF ALTERNATIVE FLOW REGIMES

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The SALMOD Chinook (*Oncorhynchus tshawytscha*) life cycle model for the Klamath River, California, USA was updated to address a number of computational and life history limitations based on over 10 years of accumulated experience. SALMOD II incorporates a complete spatial delineation of each mesohabitat unit between Iron Gate Dam and the Klamath estuary (~320 km). Mesohabitat specific relationships for Chinook spawning, fry, presmolt and immature smolt life stages are based on site specific hydrodynamic modeling from 8 representative study sites that incorporate target mesohabitat characteristics of channel width and base flow magnitude. SALMOD II was calibrated and validated to multi-year collection data and incorporated improved density dependant movement and mortality factors, a disease factor, an improved water temperature simulation model and other key life history requirements. We explain the underlying computational framework for the modeling system, highlight the spatial delineation and extrapolation methodology for mesohabitat specific habitat versus flow relationships for each Chinook life stage, and highlight important factors such as emigration and density dependant habitat movement factors.

1   BACKGROUND

SALMOD (Williamsom *et al.* [1] is a component of the Instream Flow Incremental Methodology (Stalnaker *et al.* [2] that integrates habitat limitations to a fish population through time and space (e.g., see Cheslak and Jacobson [3]. It has been broadly applied within the Klamath for a variety of research and management questions (e.g. Campbell *et al*. [4]). SALMODII was derived to address limitations in the software structure, computational efficiency and the need for additional functionality (e.g., disease, density dependant mortality and movement). Habitat quality and capacity are characterized by the hydraulic and thermal properties of individual mesohabitats (MHTs), which make up the "computational units" in the model. Model computations follow the salmonid life cycle, starting with returning adult spawners (Figure 1). Adults are spatially distributed across MHTs and incorporate factors such as redd superimposition, redd scour and dewatering. Eggs are tracked from deposition through successive life stages as a function of temperature dependant growth. Population control factors include thermal, disease, movement (freshet-induced, habitat-induced, and seasonal), and density dependant mortalities. SALMODII tracks cohorts spatially by MHT from egg deposition to a physiologically ready (e.g., immature-smolts) for estuary and ocean entry. The model operates on a daily time step and allows

multiyear simulations. Habitat capacity for each life stage is a fixed maximum number (or biomass) per unit habitat area available. Thus, the maximum number of individuals that can occupy a computational unit is calculated at each time step based on discharge, MHT type and size, and flow dependant useable habitat available (e.g., Bartholow and Henriksen [5], Hardy *et al.* [6]).

1.1 SALMOD II Computational Structure

The key life cycle framework is illustrated in Figure 1, showing the key physical and biological factors affecting size, condition and number of emigrants given a starting adult numbers.
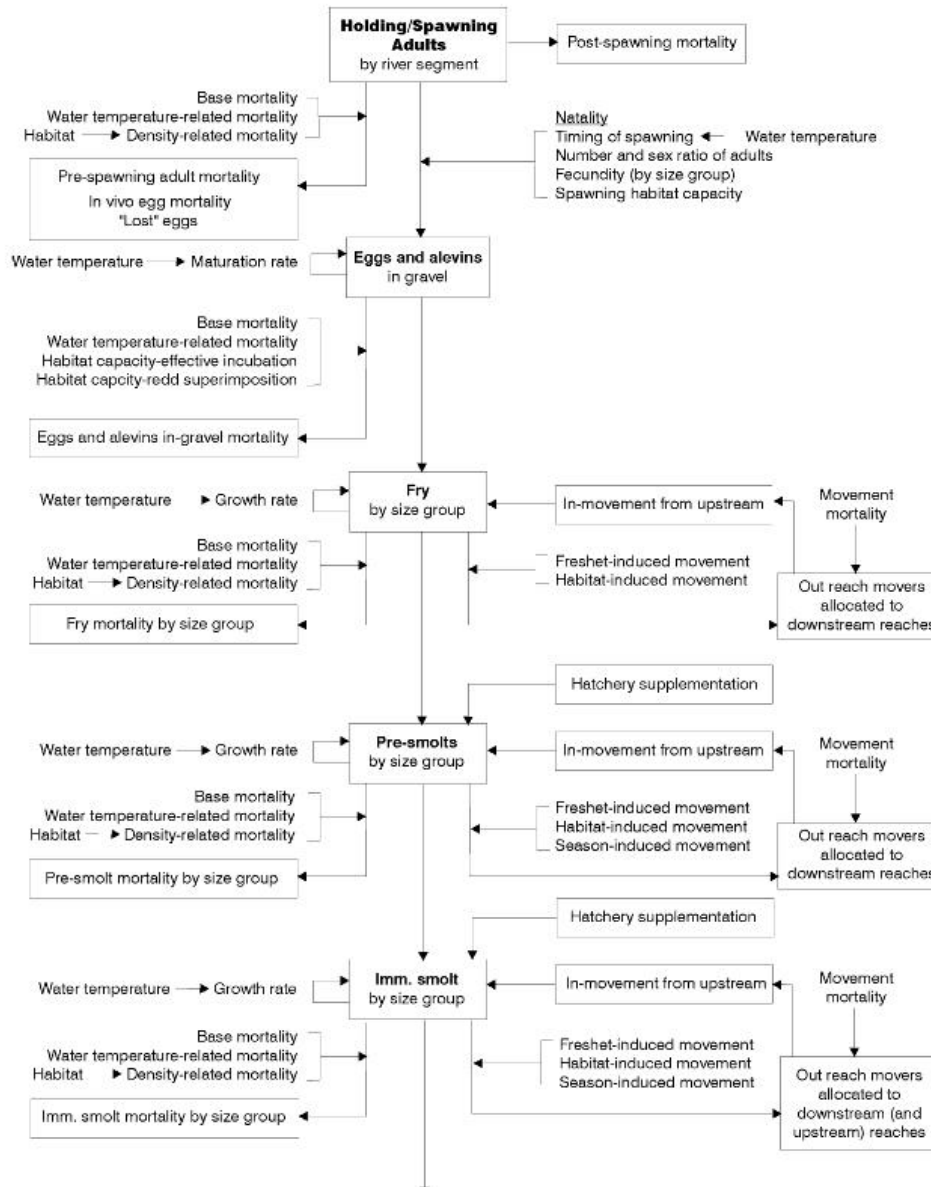

Figure 1. Computational structure of SALMOD II.

1.2 Geomorphic, Flow and Temperature Segments

The Klamath River was a priori classified into 23 reaches corresponding to output nodes of the flow and temperature model utilized by SALMOD. Geomorphic and MHT typing of the river sections relied on both

ground based measurements and aerial imagery and provided necessary inputs for the extrapolation of habitat versus flow relationships.

1.3 Defining Mesohabitat Units

The basic computational element is the mesohabitat unit (MHU). We field classified 1,600+ sequential MHUs for the 300 km main stem Klamath River between Iron Gate Dam and the Klamath River's estuary (Figure 2).
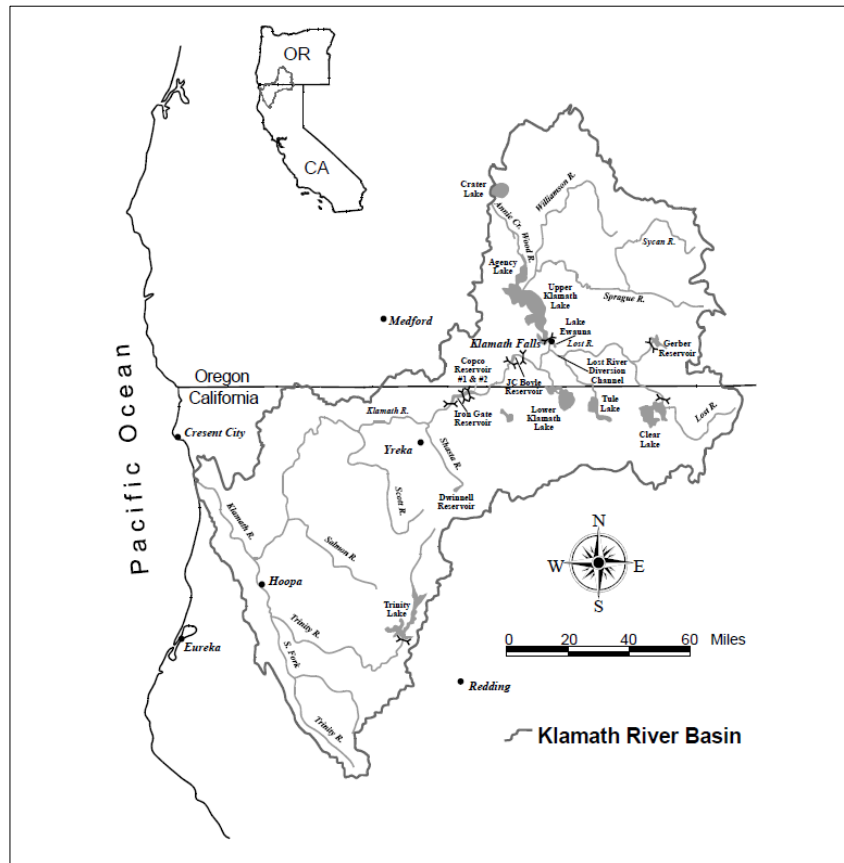

Figure 2. The Klamath Basin, located in Oregon and California, including the network of lakes, hydropower reservoirs, dams, and significant streams (figure modified from file produced by U.S. Bureau of Reclamation).

The U.S. Fish and Wildlife, Arcata Fish and Wildlife Office, U.S. Geological Survey, Fort Collins Science Center, and the Yurok Tribal Fisheries conducted the MHU inventory utilizing a stream classification system (Bisson *et al.* [7]) generalized for the Klamath River. Gradient, backwater, and channel form were the dominant hydraulic and morphologic characteristics used to classify each unique, sequential Mesohabitat Type (MHT). The survey team identified three dominant MHT slopes: Low (LS), Moderate (MS), and Steep (SS). Field classification of MHTs involved a calibration and validation, chi-square goodness of fit test validating the reliability and consistency of the slope classification scheme in the field ($p > 0.25$). The survey team delineated MHTs based on three channel configurations: Main (MA), and the two Island complexes (Split ($SP_Q \geq 0.3Q_{total}$ and $< 0.5Q_{total}$) and Side (SC) $SC_Q < 0.3Q_{total}$).

1.4 Defining Island Complexes

Island complexes were restructured in SALMODII to preserve the longitudinal spatial distances in the channel (Figure 3) and facilitate extrapolation of habitat versus flow relationships from source to target complexes (versus SALMOD see Bartholow and Henrikson [5]).
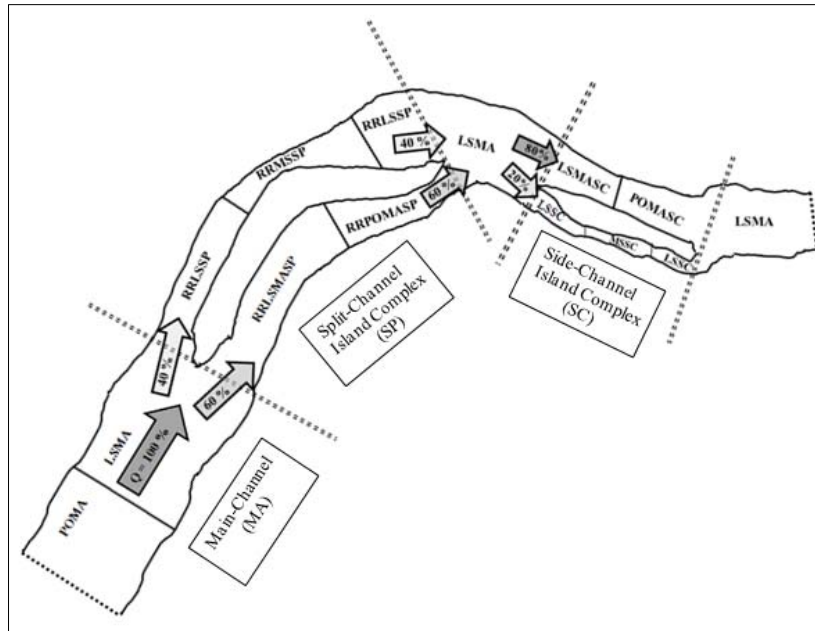
Figure 3. Channel configurations and accompanying MHT delineation for Main-Channel (MA) MHUs, along with Split-Channel (SP), and Side-Channel (SC) complexes.

1.5 MHT Specific Habitat versus Flow Relationships and Extrapolation

Resource selection functions for depth, velocity, channel index, escape cover type and distance constraints were derived from extensive multi-year sampling for spawning, fry, presmolt and immature smolt life stages. Resource functions were integrated with 2-D hydrodynamic models at eight study sites between Iron Gate Dam and the Pacific Ocean to estimate the MHT specific usable area versus flow relationships (e.g., Hardy *et al.* [6]). The study site specific MHT relationships were used as the source for scaling to target (unmeasured) MHTs. Extrapolation involved scaling the discharge range by adjusting for the addition or subtraction of the median monthly accretions longitudinally, and scaling the UA by morphological and active channel width differences between the source MHT and the target MHT. Therefore, each of the 1600+ MHTs have unique habitat versus flow relationships.

2 KEY MODEL COMPONENTS AND PROCESSES

There is insufficient space to detail all the underlying mechanistic relationships illustrated in Figure 1. However, some of the key model components and restructured processes are provided below.

2.1 Adult Migration and Spawning

Based on analysis of weir data since the 1930's adult Chinook Fall-run salmon have shifted approximately two weeks later than historical run timing (Shaw *et al.* [8]) with entry into the upper Klamath River, tributaries, and Iron Gate hatchery beginning in mid-September, peaking in early October, and concludes by the end of November. The shift is attributed to higher fall water temperatures evident after the construction of the main stem Klamath River hydropower dams and associated reservoirs. Fall Chinook spawning in the main stem Klamath River and tributaries commences in mid- October, peaking during the last week of October through the first week of November, and concluding by the end of November.

2.2 Emergence

Once main stem egg deposition occurred, incubation and emergence timing is a function of cumulative Daily Temperature Units (DTU) where water temperature exceeds 0 C. An accumulated DTU of 1,600 units is the

estimated time of emergence (Piper *et al.* [9]). Emergence timing was estimated to range between mid-February through the first week of April, with the peak occurring in March.

2.3 Fry and Juvenile Outmigration

Upon emergence, yolk-sac depletion and buttoning up, the young-of-the-year (YOY) begin their dispersal downstream as fry (< 55mm). Growth is simulated as a function of temperature and resource availability that includes density dependant factors at the MHT level. The spatial and temporal distribution of fry and juveniles in the main stem is complex due to the variability of emergence timing in the main stem, differential movement distances as a function of fish size, and variation in juveniles entering from tributaries that range from snow melt dominated to spring fed systems. The empirical outmigrant trapping data clearly illustrates this temporal variability as shown in Figure 4.
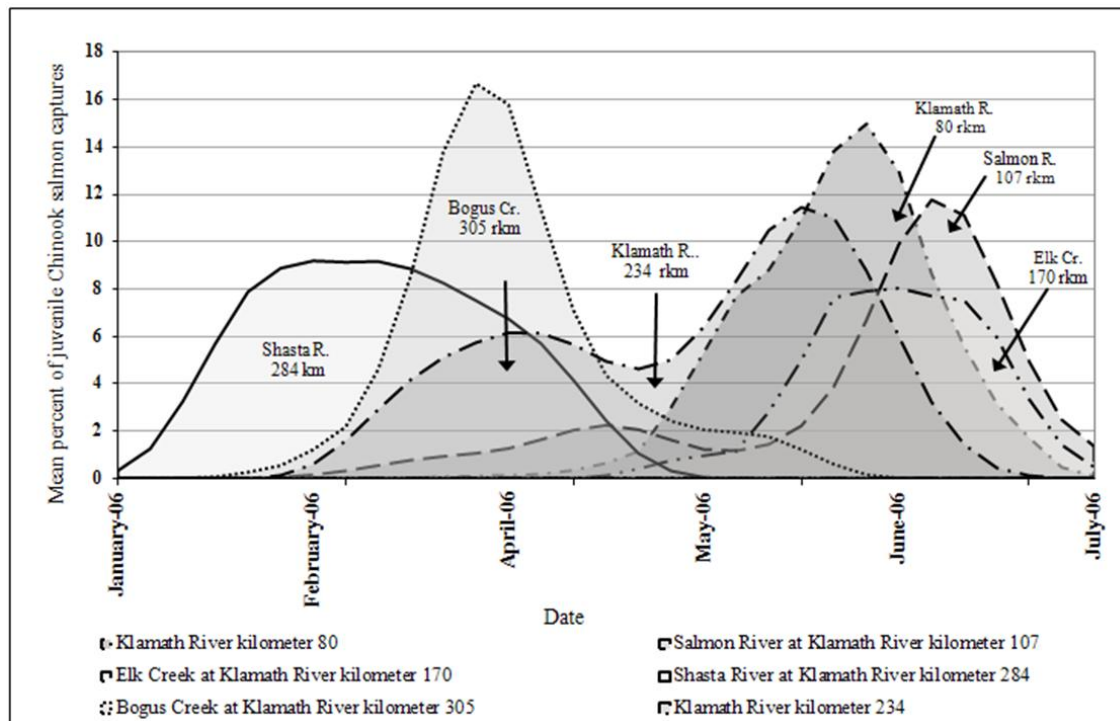

Figure 4. Outmigrant timing from key tributary sources within the Klamath River.

2.4 Movement

We modeled movement of juvenile salmon by casting a continuous advection-diffusion model in terms of the discrete MHT template. In discrete form, fish occupying MHT unit h are distributed among possible MHT units by assigning the proportion of fish in MHT unit h that move to unit i in one time step. Across all MHT units, movement proportions form a movement matrix, $\mathbf{M}$, with elements $\pi_{h,i}$ representing the probability of moving from MHT unit h to MHT unit i in one time step. Over time, movement occurs as the matrix product of MHT-specific abundance and movement probabilities:

$$\mathbf{n}(t+1) = \mathbf{Mn}(t) \tag{1}$$

where $\mathbf{n}(t)$ and is the vector of unit-specific abundances at time t and $\mathbf{n}(t+1)$ is the abundance vector after one time step ($\Delta t = 1$). We specified the movement probabilities by integrating a continuous advection-diffusion model across the discrete landscape of habitat units. An advection-diffusion model captures the well-known the tendency for a group of fish initially concentrated at a point in space to move downstream (advection) and spread out over time (diffusion; Zabel and Anderson [10]; Gurarie [11]). This process can be characterized as a traveling, widening wave (Figure 5A). One advantage of using such a model is that movement is determined by two biologically meaningful parameters: the rate of migration (r, km/d) and the rate of population spreading (σ, km^2/d). Under this model, the spatial distribution of fish originating in habitat unit h after t time steps follows a

normal distribution with mean rt and variance $\sigma^2 t$. Here, rt is the average distance moved and $\sigma^2 t$ is the variance in the spatial distribution after t time steps (Figure 6). Movement probabilities from habitat unit h are calculated by integrating the spatial distribution function between habitat unit boundaries (Figure 5B):

$$\pi_{h,i} = \int_{\Delta x_{i,\text{upper}}}^{\Delta x_{i,\text{lower}}} f\left(x \mid x_h, r, \sigma, \Delta t = 1\right) dx = F\left(\Delta x_{i,\text{lower}} \mid x_h, r, \sigma, \Delta t = 1\right) - F\left(\Delta x_{i,\text{upper}} \mid x_h, r, \sigma, \Delta t = 1\right)$$

(2)

where $\Delta x_{i,\text{upper}}$ and $\Delta x_{i,\text{lower}}$ is the distance from the midpoint of habitat unit h (x_h) to the upstream and downstream boundaries of habitat unit i, $f()$ is the pdf of the normal distribution, and $F()$ is the cdf of the normal distribution. In addition to characterizing movement in terms of the mean and variance in migration rate, this approach naturally accounts for MHT units of different length (Figure 3). Many different models of movement can be constructed from this general movement framework by allowing r and σ to vary with environmental or individual covariates. For example, Zabel [12] found that both r and σ were positively related to fish size manifested in increased migration rates as fish transitioned from parr to smolts. The rate of diffusion also increased with fish size as expected. MHT specific density-dependent movement is represented when r increases with fish density, and flow-related movement is given when r increases with river flow or velocity. This movement framework can also be used to simulate upstream migration of adults. Last, setting $r = 0$ and $\sigma \geq 0$ simulates a resident non-migratory population that moves among MHTs but exhibits no net population displacement.
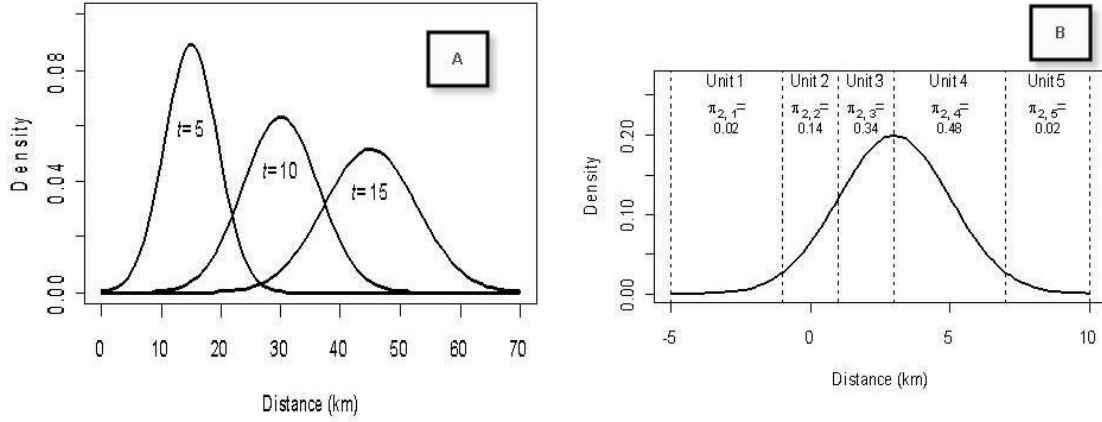

Figure 5. A: The spatial distribution of a population after t = 5, 10, and 15 days for a starting point of x = 0, a migration rate of 3 km/d, and a standard deviation of 2 km^2/d. B: Example illustrating how the advection-diffusion model is mapped to discrete space to calculate movement probabilities. The solid line shows the spatial distribution of fish originating in habitat unit 2 (x = 0) after migrating for one day at a migration rate of 3 km/d and a standard deviation of 2 km^2/d. Dashed lines show the location of habitat unit boundaries relative to the mid-point of habitat unit 2. The area under the spatial distribution curve between habitat unit boundaries yields $\pi_{h,i}$, the probability of moving from unit h to unit i in one time step. For example, the probability of moving from unit 2 to unit 4 ($\pi_{2,4}$) is 0.48, whereas the probability of remaining in unit 2 ($\pi_{2,4}$) is 0.14.
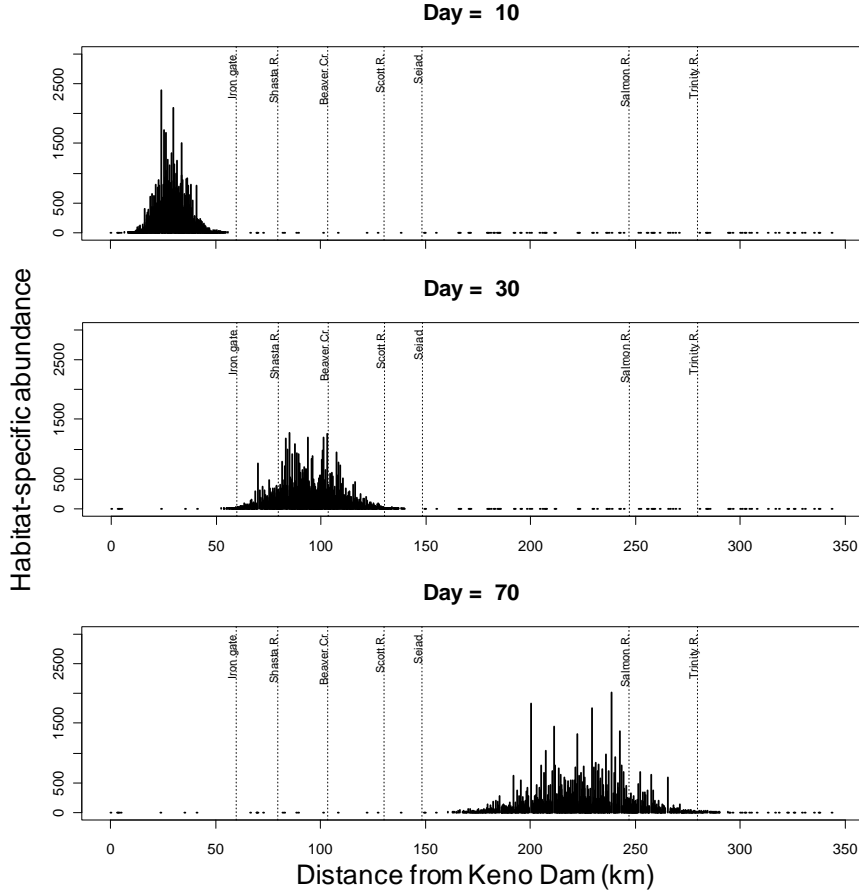
Figure 6. Modeled outmigrant distributions in time and space in the Klamath River.

3   RESULTS

Density Dependent Survival

We use a multi-stage Beverton-Holt model to capture density-dependent effects on survival (Moussalli and Hilborn [13]). It is derived from theory about foraging, predation risk, and territorial behavior typical of juvenile Chinook salmon (Walters and Korman [14]). For life stage s in MHT unit h, the relationship is:

$$N_{sh}(t+1) = \frac{N_{sh}(t)}{\frac{1}{S_1} + \frac{N_{sh}(t)}{c_{sh}A_{sh}}}$$

(3)

Where $N_{sh}(t)$ is the number of individuals at time t, $N_{sh}(t+1)$ is the number surviving after one time step, S_1 is survival over a single time step due to all density-independent sources (e.g., thermal tolerance or disease), c_{sh} is the habitat capacity of life stage s in unit h (expressed as number/m^2), and A_{sh} is the habitat area (m^2) available to life stage s in habitat unit h. Survival due to both density dependent and independent sources is then:

$$S_{sh} = \frac{N_{sh}(t+1)}{N_{sh}(t)} = \frac{1}{\frac{1}{S_1} + \frac{N_{sh}(t)}{c_{sh}A_{sh}}}$$

(4)

Two key parameters in this model are A_{sh} and c_{sh}: A_{sh} quantifies the amount of optimal habitat in a given habitat unit, whereas c_{sh} quantifies habitat capacity in terms of the maximum fish density within optimal habitat. Habitat area in a given unit varies with flow and influences densities of juvenile salmon occupying optimal habitat. We relate maximum fish density to fish size via the well-known relation between territory size and fish size. Grant and Kramer [15] showed that territory size is a good predictor of maximum densities of juvenile salmonids in streams. We use their allometric relationship to determine c_{sh}, given the mean size of juveniles in

life stage s and habitat unit h (Figure 7A). Given the size-dependent maximum density and the available habitat in a given unit as a function of flow at time t, the product of c_{sh} and A_{sh} yields the total number of fish that the optimal habitat can support.

Example - The Beverton-Holt survival relationships at 28.3 cms, 141.6 cms, and 198.2 cms were computed for MHT unit 624, a SEPOMASC (length 752 meters; width 130 meters). The associated available habitats were (Ash) were 242 m2, 914 m2, and 1794 m2 respectively. We assumed a density independent survival (SI) of 0.98 d-1 and a mean fry size of 40 mm, resulting in a maximum density of 18.1 fry/m^2. The corresponding fry capacities in this MHT at these discharges were 4384, 16585, and 32552 fry. The Beverton-Holt curves illustrate the effect habitat capacity on density-dependent survival (Figure 8A). At low abundance (e.g., < 2000 fry), the number of surviving fry is similar among flows. However, as the number of fry increase, survival decreases sharply for the low flow scenario as carrying capacity is approached (Figure 8B). For the high flow scenario, survival is less than expected under solely density independent survival even when fry abundance remains well below capacity. This example illustrates how density dependence operates at abundances well below carrying capacity.
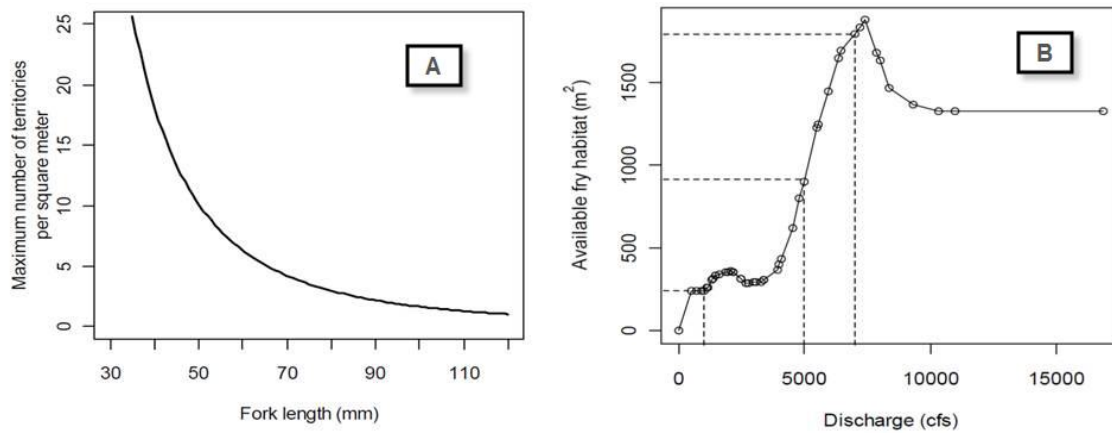

Figure 7. A: Maximum number of territories per square meter as a function of fish size, which was used to estimate habitat capacity. This relationship was based on a territory-fish size relation for juvenile salmon developed by Grant and Kramer (1990). B: Usable habitat area versus flow for habitat unit 624, a SEPOMASC meso-habitat type near Seiad Creek on the Klamath River. Dashed lines show three flows selected for plotting density-dependent survival relationships.
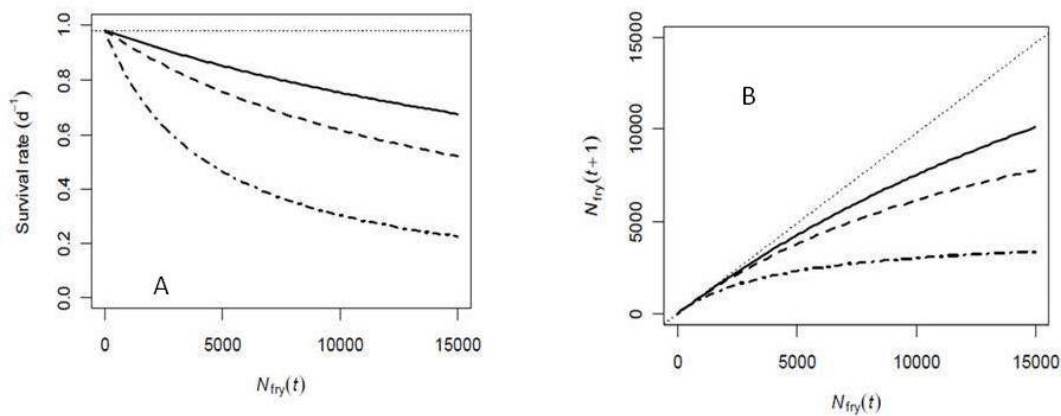

Figure 8. Beverton-Holt relationship for three flows showing the number of surviving fish (A) and survival (B) as a function of the number of fry residing in the habitat unit. The solid, dashed, and dot-dashed lines are for the high, medium, and low flow, respectively. The light dotted line shows the relationship for density-independent survival at a rate of 0.98 d^{-1}.

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