MODELING FISH MOVEMENT IN A SPATIALLY EXPLICIT POPULATION MODEL OF JUVENILE CHINOOK SALMON IN THE KLAMATH RIVER, USA

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Movement of individuals through space is a common feature of life cycle models that simulate the effects of spatial variation in the environment on population dynamics. Movement models range in biological realism from simple meta-population models that keep track of the number of individuals in each sub-population to complex individual based approaches that keep track of the *xy*-coordinates of each individual in continuous space. We present an approach that is intermediate between these two extremes. We simulated movement of juvenile Chinook salmon by casting a continuous advection-diffusion model in terms of a discrete habitat template that represents the river as a mosaic of meso-habitat units. Movement is achieved by assigning the probability that fish in habitat unit h move to unit i in one time step. These movement probabilities are determined by integrating the advection-diffusion model between habitat unit boundaries. This approach has a number of advantages. First, 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). Second, this movement model naturally accounts for variation in the model's spatial (e.g., length of each habitat unit) or temporal (e.g., daily or weekly) resolution. Last, many different models of movement can be constructed from this general framework by allowing r and σ to vary with environmental or individual covariates. We illustrate application of this model to juvenile Chinook salmon in the Klamath River, USA, where movement rate varies as a function of fish density and size in each habitat unit.

1 MODELING FRAMEWORK OF THE STREAM SALMONID SIMULATOR

The Stream Salmonid Simulator (S3) is a spatially explicit model that is currently being developed to track abundance of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) as they migrate from natal areas to the ocean. The heart of the S3 model is the dynamic simulation of movement and survival of juvenile salmon during freshwater rearing in a river environment. The S3 model tracks the number of individuals by habitat unit, date, life stage, and source population. Formally, we define this quantity as $n_{p,s}(h, t)$ where:

n = number of individuals
p = source population, $p = 1, \ldots, P$
s = life stage, s = fry, parr, or smolt, for example
h = habitat unit, $h = 1, \ldots, H$
t = day (or date), $t = 1, \ldots, T$.

As this notation implies, S3 is a discrete-space, discrete-time model that runs on a daily time step. Spatially, the continuous longitudinal axis of the river is divided into a series of discrete spatial units of length $\Delta x_h = x_{h,\mathrm{up}} - x_{h,\mathrm{down}}$, where x is the distance from the downstream terminus of the model (the river's mouth) and $x_{h,\mathrm{up}}$ and $x_{h,\mathrm{down}}$ mark the upstream and downstream boundaries of habitat unit h. Source populations represent individuals entering the model's domain from different tributaries or from emerging fry that are progeny of spawning adults within the mainstem river.

The dynamics of the model operate much like a stage-structured matrix population model that is governed by a series of transition equations. Transition equations consist of daily survival, movement probabilities, and a growth function that determines when fish grow large enough to transition from one life stage to the next. In terms of order of operations, fish in habitat h on day t survive, grow, and then move. In this paper, we focus on modeling downstream movement within the S3 modeling framework.

2 MODELING MOVEMENT

To implement movement, fish occupying habitat unit h are distributed among possible habitat units by assigning the proportion of fish in habitat unit h that move to unit i in one time step. Across all habitat units, movement proportions form a movement matrix, **M**, with elements $\pi_{i,h}$ representing the probability of moving from habitat unit h to habitat unit i in one time step. Thus, **M** is an HxH matrix with columns (indexed by h) representing habitat units from which fish move and rows (indexed by i) representing the habitat units to which fish may move. Furthermore, the columns of **M** sum to one.

Over time, movement is implemented as the matrix product of habitat-specific abundance and movement probabilities:

$$\mathbf{n}_{p,s}(t+1) = \mathbf{M}_{p,s}\mathbf{n}_{p,s}(t) \qquad (1)$$

where $\mathbf{n}_{p,s}(t)$ is the vector of habitat unit-specific abundances at time t for each source population and life stage, and $\mathbf{n}_{p,s}(t+1)$ 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 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 [1]; Gurarie [2]). This process can be characterized as a traveling, widening wave (Figure 1). 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 1).

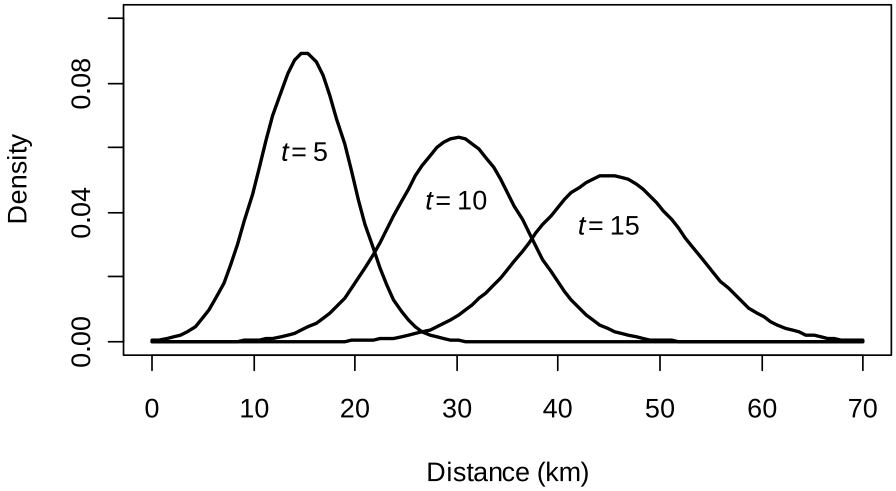

Figure 1. The spatial distribution of a population after t = 5, 10, and 15 days for a starting point of x = 0, a migration rate of 3 km/d, and a standard deviation of 2 km^2/d.

Movement probabilities from habitat unit *h* are calculated by integrating the spatial distribution function between habitat unit boundaries (Figure 2):

$$\pi_{i,h} = \int_{\Delta x_{i,\mathrm{up}}}^{\Delta x_{i,\mathrm{down}}} f\left(x \mid x_h, r, \sigma, \Delta t = 1\right) dx = F\left(\Delta x_{i,\mathrm{down}} \mid x_h, r, \sigma, \Delta t = 1\right) - F\left(\Delta x_{i,\mathrm{up}} \mid x_h, r, \sigma, \Delta t = 1\right) \qquad (2)$$

where $\Delta x_{i,\mathrm{upper}}$ and $\Delta x_{i,\mathrm{lower}}$ 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 habitat units of different length (Figure 2). Figure 3 shows an example of applying this movement model within the framework of Klamath River S3 model.

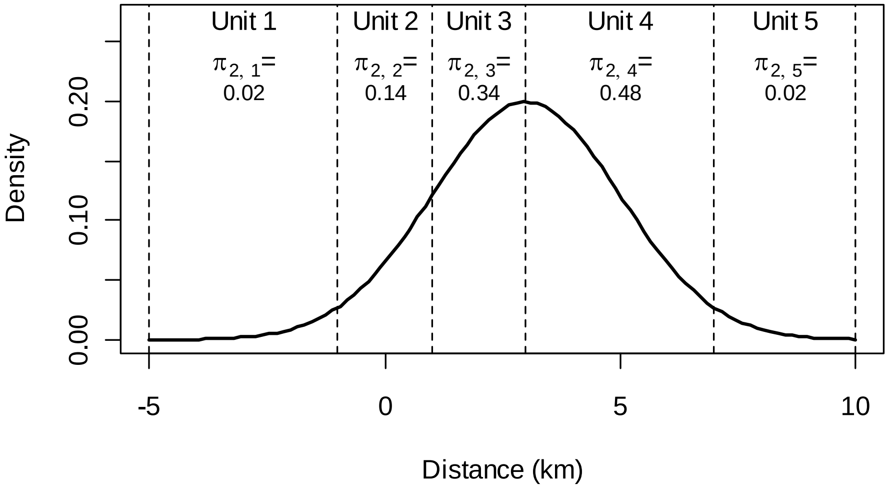

Figure 2. Example illustrating how the advection-diffusion model is mapped to discrete space to calculate movement probabilities. The solid line shows the spatial distribution of fish originating in habitat unit 2 ($x = 0$) after migrating for one day at a migration rate of 3 km/d and a standard deviation 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.

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 [3] found that both *r* and σ of fall Chinook salmon in the Snake River was positively related to fish size. These findings show that not-only did migration rates increase with size as fish transitioned from parr to smolts, but that the rate of diffusion also increased with size. Other interesting movement relationships include density-dependent movement where *r* increases with fish density in a given habitat, and flow-related movement, where *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 habitats but exhibits no net population displacement. These examples show how an advection-diffusion model of movement provides a flexible framework for simulating movement of salmon.

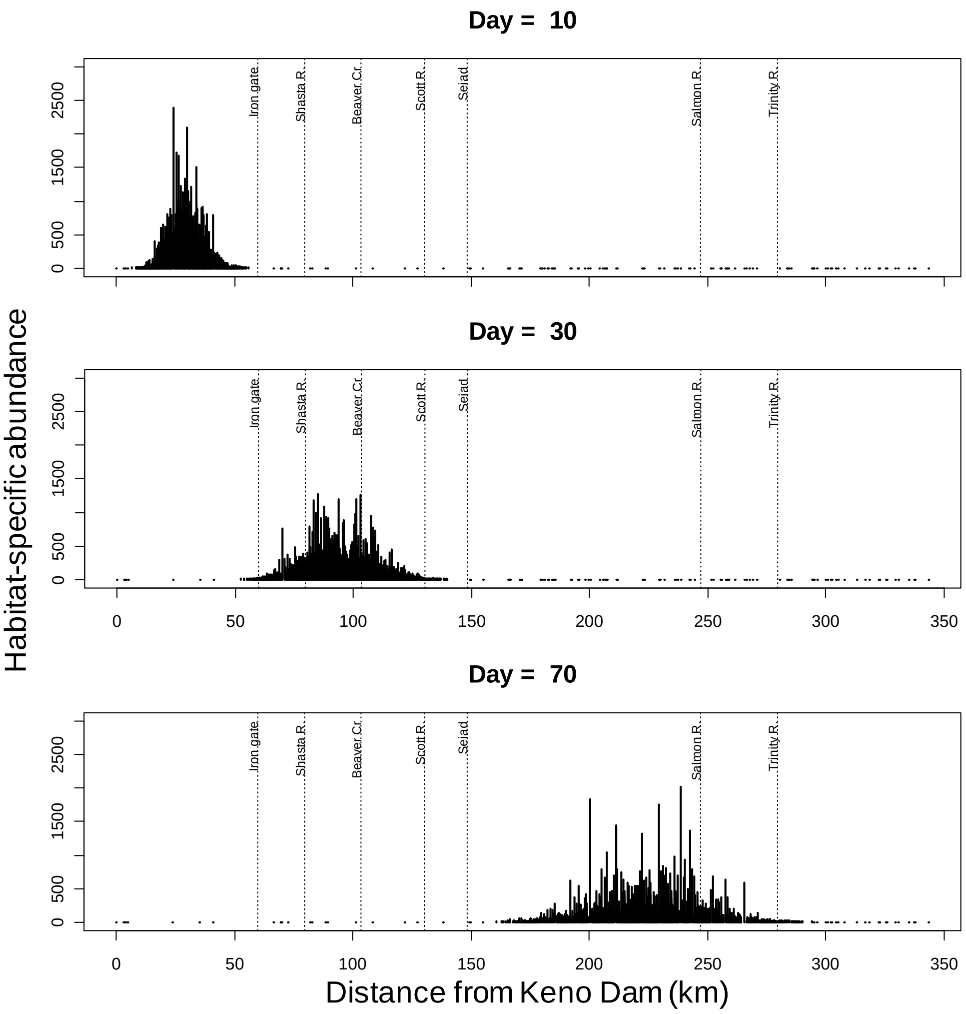

Figure 3. Example of the movement model implemented for the Klamath River. Shown is the spatial distribution after 10 d, 30 d, and 70 d for a group of fish "released" at km 0 with a mean migration rate of 3 km/d and a standard deviation of 3 km^2/d.

ACKNOWLEDGEMENTS

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