

Predicting the effects of currents on the adaptive movement of juvenile salmonids

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ABSTRACT

Background: Anadromous salmonids present a marvellous opportunity to study animal movement, with some juveniles in the Yukon and Amur rivers travelling more than 2000 km from their natal areas to the ocean. During their freshwater residence, juvenile salmonids, regardless of river of origin or migration distance, balance the pressures of feeding, predator avoidance, and migration to survive.

Questions: What are the choices of current and swimming velocities that stream-dwelling juvenile salmonids use to optimize lifetime reproductive success? How are these influenced by maximum current velocity in the stream or river that they inhabit?

Mathematical methods: I developed a dynamic optimality model that treats current and swimming velocities as decision variables. The state variables are downstream river location and fish size. I solve the optimality model using optimal control theory and apply it to juvenile ocean-type Chinook salmon in the Hanford Reach, Columbia River, Washington.

Results: Five fundamental behaviours or movement phases result from the optimality model: rapid upstream migration, appetitive (‘foraging’) upstream movement, station holding, appetitive downstream movement, and rapid downstream migration. These fundamental behaviours were not specified *a priori*, but emerge when optimizing lifetime reproductive success over the full range of possible behaviours. The appetitive and station holding behaviours are broadly characterized as foraging/predator avoidance. Rapid migration is favoured over foraging/predator avoidance whenever the magnitude of the marginal value of displacement exceeds the marginal predation risk of displacement. If, during foraging/predator avoidance, the maximum current velocity rises above the swimming speed that maximizes growth, station holding is optimal; otherwise, appetitive movement, which carries greater predation risk, might be optimal. The two types of downstream movement predicted by the optimality model (appetitive movement and rapid downstream migration) describe the movements of the ‘ocean-type’ and ‘stream-type’ races of Chinook salmon populations of the Columbia River. In the Hanford Reach application, optimal movements begin with station holding, then switch to downstream appetitive movement or rapid downstream migration, depending on the maximum current velocity. Juveniles accelerate as they migrate downstream. I describe an experiment to test the influence of current velocity on foraging behaviour and a field study to characterize juvenile upstream migrations.

Keywords: behavioural ecology, bioenergetics, freshwater ecology, migration, optimal control, predation, salmonids.

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INTRODUCTION

A main goal of movement ecology is to partition an animal's movement path into a series of discrete phases that change over time as a response to its changing environment, developmental stage, and immediate responses to demands for survival, feeding, and reproduction (Nathan *et al.*, 2008). Juvenile anadromous salmonids are a magnificent study organism, with some individuals in the Yukon and Amur rivers migrating more than 2000 km from rearing areas to the sea (Quinn, 2018). Individuals might travel many times that distance during their ocean residence, and then return to spawn and die in the same rivers and streams where they hatched (Healey, 1991; National Research Council, 1996). Studies that divided the movement path of salmon into phases began in earnest in the 1990s (Mangel, 1994; Mangel and Satterthwaite, 2008; Satterthwaite *et al.*, 2009). These studies tackled behaviour from an adaptationist perspective, seeking behaviours that maximized expected lifetime reproductive success (Mangel and Clark, 1988).

These early studies did not predict fine-scale movements over the entire freshwater period of a juvenile salmonid. Questions that can be answered only with a fine-scale movement model include:

1. Migration can take place in slow or swift currents, and at day or night – which of these behaviours is optimal, and under what conditions?
2. What impact do slowed river currents have on feeding, predator avoidance, and migration?

This last question is increasingly important because dams, irrigation withdrawals, and climate change can all slow river currents that juveniles depend on for food delivery and migration (Independent Scientific Group, 1999; Quinn, 2018). In some instances, current velocity is directly manipulated for the benefit of juvenile salmonids (Langshaw *et al.*, 2018).

To predict fine-scale movements, I develop an optimality model that uses current and swimming velocities as decision variables. I refer to current velocity as a decision variable, as shorthand for saying that a fish chooses the current velocity in which it swims. The velocity choices allow a continuum of possible behaviours, ranging from station holding to rapid migration (upstream or downstream). I build upon optimal foraging theory, which casts net energy gain as a function of swimming velocity (required to hold station) in a current delivering food in the form of invertebrate drift (Fausch, 1984, 2014; Hughes, 1998; Piccolo *et al.*, 2014). My approach goes beyond optimal foraging theory, and I seek strategies that balance the pressures of foraging, predation risk (Gilliam, 1982; Werner and Gilliam, 1984; Gilliam and Fraser, 1987), and migration (Dingle and Drake, 2007).

My goal is to construct a simple optimality model to determine a suite of stream-dwelling juvenile salmonid behaviours (or movement phases) that maximize lifetime reproductive success, where behaviours are characterized by current and swimming velocity choices. I also seek the conditions that determine which behaviour or movement phase is predicted by the model at any given instant, focusing primarily on the role of maximum current velocity. I first develop equations that describe the selective forces acting on a juvenile salmonid (these vary with fish size, location, and velocity choices), then determine the behaviours that maximize lifetime reproductive success (Mangel and Clark, 1988; Davies *et al.*, 2012). I use Pontryagin's Maximum Principle (Lenhart and Workman, 2007) to maximize lifetime reproductive success (Oster and Wilson, 1978; Smith, 1978; Gilliam, 1982; Clark, 1990). I then compare the optimal behaviours predicted by the optimality model to observed behaviours of juvenile salmonids, including those of the 'ocean-type' and 'stream-type' races of Chinook salmon of the Columbia River (Gilbert, 1913).

MOTIVATION: CHINOOK SALMON IN HANFORD REACH, COLUMBIA RIVER, WASHINGTON

I apply a simplified version of the optimality model to ocean-type Chinook salmon (*Oncorhynchus tshawytscha*) in the Hanford Reach of the Columbia River (Fig. 1), and vary the maximum current velocity to gauge its effect on adaptive movements. The Hanford Reach, which extends from Priest Rapids Dam (river km 639) to the city of Richland, Washington (river km 545), is the last free-flowing reach of the mainstem Columbia River above Bonneville Dam and within the United States (Becker, 1985; Dauble and Watson, 1997). Although many salmon populations in the Columbia River Basin are listed under the US Endangered Species Act of 1973, the Hanford Reach ocean-type Chinook salmon population is one of the 99 ‘healthy native stocks’ of salmon and steelhead in the Pacific Northwest and California, and one of 20 stocks considered to be at least two-thirds as abundant as it would be without human impact (Huntington *et al.*, 1996; Dauble and Geist, 2000).

Understanding the impacts of slowed river currents on juvenile salmon feeding, predator avoidance, and migration is important in the Columbia River, because its flow regime has changed tremendously over the last century. The mean virgin flow at The Dalles (river km 309) has decreased by 8–9% due to climate change and 7–8% due to water withdrawals. Flow regulation since the 1970s has reduced peak spring flows by about 45% and increased flow during the rest of the year. The decrease of the spring freshet flow due to climate change is 11%; due to withdrawal, 12%; and due to flow regulation, 26% (Naik and Jay, 2011).



Fig. 1. Map of Hanford Reach of the Columbia River and vicinity.

OPTIMALITY MODEL

I assume that decision-making by organisms is a state-dependent dynamic process involving immediate and future consequences of decisions on survival and reproduction (Krebs and Kacelnik, 1991). To produce insights and build intuition without resorting immediately to simulation, I construct a simple model that balances ecological realism and mathematical tractability. Such a model may prove useful for understanding the results of more complex models, such as Individual-Based Models (IBMs) (Goodwin *et al.*, 2006; Benson *et al.*, 2021).

The optimality model developed here stands in contrast to complex IBMs that incorporate many more details than the optimality model. In the same way that a topographic map does not capture every detail of a landscape but is essential for a successful traverse of a complex landscape, analysis of the optimality model captures key details for understanding the topography of fitness. Furthermore, IBM models rely on computer simulation and are not amenable to mathematical analysis. In particular, with simulation, it may be impossible to discover what assumptions are responsible for the conclusions (Roughgarden, 2012). IBMs do not yield the general understanding that can be obtained by mathematical analysis, which describes behaviour across all possible parameter combinations (Cornell *et al.*, 2019). The real contribution of mathematics is its precise qualitative framework of reasoning, which, when applied to biological problems, can provide the theories needed to guide experiments and interpret experimental results (Bingham and Asquith, 2001).

Current velocity, swimming velocity, and duration of freshwater residence are decisions that describe a range of possible behaviours. The decisions, although made during the early life history of a fish, influence survival over a fish's entire life history: from early freshwater residence, to ocean residence, to a return to freshwater to spawn. Although some anadromous salmonids, such as Atlantic salmon (*Salmo salar*) (Aas *et al.*, 2011) and steelhead (*O. mykiss*) (Keefer *et al.*, 2008) are iteroparous, I consider only females of populations that are semelparous, but the model can be extended to treat males and iteroparous species as well.

The dynamic optimization model I develop for salmon behaviour is formulated as an optimal control problem (Gilliam, 1982; Clark, 1990; Lenhart and Workman, 2007), and I solve it using Pontryagin's Maximum Principle (Pontryagin *et al.*, 1962). The model consists of two control variables and a control parameter, two control variable constraints, two state variables, and a metric of fitness (Table 1). I use assumptions that simplify the analysis while capturing trade-offs among migration, growth rate, and survival rate.

Control variables: current and swimming velocities

At any instant, t , a juvenile chooses the current in which it swims (and hence is choosing a current velocity, $u(t)$), and its swimming velocity, $v(t)$. Cross-sectional current velocity is typically zero at the shoreline and maximal midstream (Marchand *et al.*, 1984; Gall, 1993). The current velocity that a juvenile chooses cannot be greater than the maximum current velocity at its position at time t ; letting $X(t)$ denote the position (displacement from the point of emergence) of the juvenile at time t , this means

$$0 \leq u(t) \leq u_{\max}(X(t), t). \quad (1)$$

Swimming velocity, $v(t)$, which is measured relative to current velocity, is constrained so that its absolute value (i.e. swimming speed) ranges from zero to the fatigue speed of a fish,

$$|v(t)| \leq v_{\max}(X(t), W(t), t). \quad (2)$$

Table 1. Notation used in optimality model and its solution

Variable or function	Description
t	Time
$u(t)$	Current velocity (control variable)
$v(t)$	Swimming velocity (control variable)
$X(t)$	Displacement (state variable)
x_f	Distance from point of emergence to ocean
$W(t)$	Fish weight (state variable)
w_0	Initial fish weight
$u_{\max}(X, t)$	Maximum current velocity
$v_{\max}(X, W, t)$	Maximum swimming velocity
$g(v, X, W, t)$	Freshwater growth rate
t_f	Time that a juvenile arrives in the ocean, which may be free or fixed in the optimization
$\theta(X, t)$	Predator density
$k(X, W, t)$	Capture probability
$\mu_0(X, W, t)$	Base mortality rate
$v_g(X, W, t)$	Swimming velocity that maximizes growth (maximum growth velocity)
$\lambda_1(t)$	Costate variable associated with displacement
$\lambda_2(t)$	Costate variable associated with weight
$H(u, v, X, W, \lambda_1, \lambda_2, t)$	Hamiltonian function
$H^*(X, W, \lambda_1, \lambda_2, t)$	Hamiltonian maximized with respect to arguments u and v
$u^*(X, W, \lambda_1, \lambda_2, t)$	A value of u that, together with v^* , maximizes the Hamiltonian at $(X, W, \lambda_1, \lambda_2, t)$
$v^*(X, W, \lambda_1, \lambda_2, t)$	A value of v that, together with u^* , maximizes the Hamiltonian at $(X, W, \lambda_1, \lambda_2, t)$
$J(u, v, t_f)$	Logarithm of lifetime reproductive success (fitness measure)
$\Phi(W(t_f), t_f)$	Terminal future reproductive success
$\sigma_1 = \lambda_1 + \theta k$	A switching function that is zero at the boundary for rapid upstream migration. It represents the slope of the left-hand piece of the piecewise linear functions $Y(u)$ and $L(v)$
$\sigma_2 = \lambda_1 - \theta k$	A switching function that is zero at the boundary for rapid downstream migration. It represents the slope of the right-hand piece of the piecewise linear functions $Y(u)$ and $L(v)$
$Y(u)$	A piecewise linear function of u used to maximize the Hamiltonian. It is formed by treating v as fixed in the Hamiltonian
$u^*(v)$	The function that returns the optimal current velocity choice as a function of v
$L(v)$	A piecewise linear function of v used to maximize the Hamiltonian. It is formed by plugging $u^*(v)$ into $Y(u)$
$H(v)$	The Hamiltonian that is formed by substituting $u^*(v)$ for u in the original Hamiltonian, thus transforming a two-dimensional optimization problem into a one-dimensional problem
λ_1^{crit}	Critical value of the costate variable that defines the point at which the optimal behaviour switches from station holding or appetitive upstream movement ($\lambda_1 < \lambda_1^{\text{crit}}$) to downstream appetitive movement ($\lambda_1 > \lambda_1^{\text{crit}}$). This critical value lies in the interval $(0, \theta k)$ and applies only when $u_{\max} < v_g$ (Fig. 6)

where $W(t)$ is fish weight at time t , and $v_{\max}(X(t), W(t), t)$ is the fatigue speed of a fish of mass $W(t)$ and location $X(t)$.

I let positive displacement denote downstream movement and negative displacement denote upstream movement. Therefore, a fish swimming against the current has a negative swimming velocity, while a fish swimming with the current has a positive swimming velocity. A juvenile salmonid controls its upstream or downstream movement by adjusting its current and swimming velocity choices over time. When $v(t) + u(t) = 0$, the juvenile holds station; when $v(t) + u(t) < 0$, it moves upstream; and when $v(t) + u(t) > 0$, it moves downstream. For notational convenience, the time argument for the control variables is sometimes suppressed, and they are written as u and v .

Dynamics of the state variables

Displacement of a juvenile from the point of emergence is governed by a differential equation that depends on both current and swimming velocity choices:

$$\frac{dX}{dt} = u(t) + v(t). \quad (3)$$

The initial displacement is $X(t_0) = 0$, where t_0 is the time at emergence. The final displacement is $X(t_f) = x_f$, where t_f is the time at ocean entry and x_f is the distance from the point of emergence to the ocean.

The weight of a juvenile salmonid is governed by a differential equation based on energy intake and costs. Energy intake depends on feeding behaviour, which involves an inherent trade-off. When a fish is inactive (i.e. its swimming velocity is zero), it obtains no food and its weight declines because there is an energetic cost of routine maintenance. When a fish is too active (i.e. swimming velocity is too high), metabolic cost overtakes the benefit of greater food intake, and again, weight declines (Bachman, 1982). These features are captured by assuming that growth rate, g , is a concave function of swimming speed. This makes growth rate a double-humped function of swimming velocity that is symmetric about the vertical axis (Fig. 2). Such concave growth functions were developed for pelagic predators (Ware, 1975, 1978), and have been applied to drift feeders in streams (Bachman, 1982; Addley, 1993; Guensch *et al.*, 2001).

Weight changes according to

$$\frac{dW}{dt} = g(v, X, W, t), \quad (4)$$

where the initial weight is $W(t_0) = w_0$ at emergence (time t_0). The variables X and t are included as arguments of g to capture the spatial and temporal patterns in food availability and metabolic costs.

Freshwater survival rate

Predation is the main cause of juvenile mortality after emergence, and heavy predation losses have been documented (Foerster and Ricker, 1941; Hunter, 1959; Vigg and Burley, 1991). I assume that predation is directly influenced by the choices of current and swimming velocity. During a small interval of time Δt , the probability of encountering a predator is

$$\Pr\{\text{encounter in } [t, t + \Delta t]\} = |u(t) + v(t)|\theta(X, t)\Delta t, \quad (5)$$

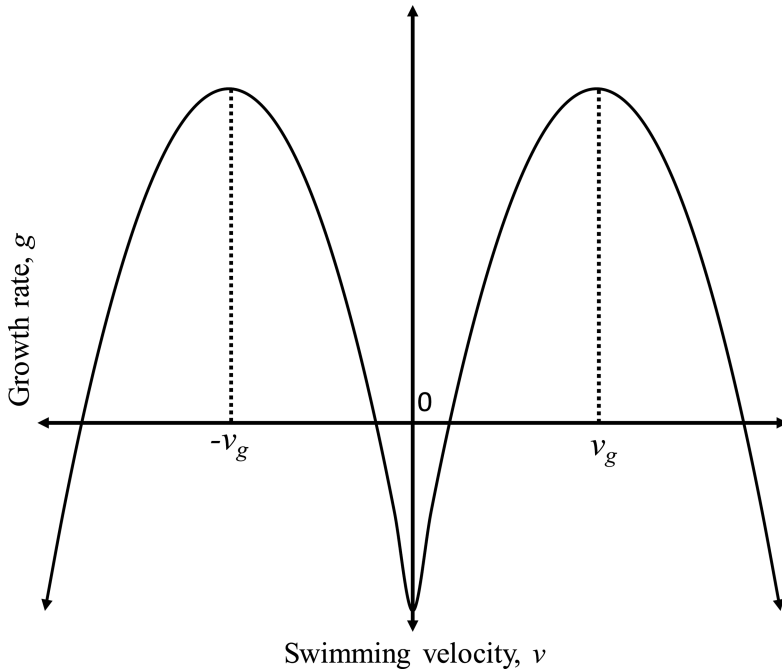


Fig. 2. A typical growth curve as a function of swimming speed. The curve is a double-humped function of swimming velocity, v , symmetric about $v = 0$, and obtains its maximum value at $-v_g$ (swimming in the upstream direction) and v_g (swimming in the downstream direction). Swimming velocity is measured relative to the current, not the streambed.

where $\theta(X, t)$ is the predator density (the average number of predators per unit distance). When a predator is encountered, the probability that the juvenile is captured and killed, $k(X, W, t)$, is a function of position, juvenile weight, and time. Quinn (2018) argues that mortality during the juvenile stage is mainly predation driven, and that mortality decreases with size (Hartman *et al.*, 1987; Hume and Parkinson, 1988; Smith and Griffith, 1994; Quinn and Peterson, 1996). Water temperature also influences predation rate (e.g. Vigg and Burley, 1991; Tabor *et al.*, 1993). The effect of water temperature on predation can be included directly in the capture probability since it is allowed to vary with time and position.

If $\mu_0(X, W, t)$ is the base mortality rate, the probability of death in the interval $[t, t + \Delta t]$ is given by

$$\Pr\{\text{death in } [t, t + \Delta t]\} = [|u(t) + v(t)|\theta(X, t)k(X, W, t) + \mu_0(X, W, t)]\Delta t. \quad (6)$$

Given the rate of mortality in equation (6), the probability of survival from emergence to ocean entry is (Hilborn and Mangel, 1997):

$$S(t_f) = \exp\left(-\int_{t_0}^{t_f} (|u + v| \theta k + \mu_0) dt\right), \quad (7)$$

where I suppress the time and state arguments of the functions in the integrand for notational convenience; and time of ocean entry, t_f , is either fixed or free to be chosen optimally.

Terminal future reproductive success

Terminal future reproductive success is determined by ocean survival, upstream survival, and egg production at the time of spawning, which are functions of the time of ocean entry, t_f , and the weight at ocean entry, $W(t_f)$. Thus, the logarithm of terminal future reproductive success is

$$\Phi(W(t_f), t_f) = \log(\text{ocean survival} \times \text{upstream survival} \times \text{fecundity}). \quad (8)$$

I assume that $\Phi(W(t_f), t_f)$ increases with $W(t_f)$. For salmon, this assumption is consistent with the observation that smolt-to-adult survival rate increases with size (Koenings *et al.*, 1993); moreover, if a larger size at ocean entry is carried into adulthood, average fecundity will also be greater (Healey and Heard, 1984).

Fitness measure

Considering females only, the fitness measure, J , is the logarithm of lifetime reproductive success, namely:

$$J = \log(\text{survival from emergence to ocean-entry} \times \text{ocean survival} \times \text{upstream survival} \times \text{fecundity}). \quad (9)$$

I use the logarithm of lifetime reproductive success instead of lifetime reproductive success for mathematical convenience; the optimal behaviours are unaltered by this transformation.

Thus, the fitness measure from emergence to spawning is

$$J(u, v, t_f) = - \int_{t_0}^{t_f} [u(t) + v(t) | \theta(X, t) k(X, W, t) + \mu_0(X, W, t)] dt + \Phi(W(t_f), t_f), \quad (10)$$

where the time argument of X and W in equation (10) is suppressed for notational convenience. The time of arrival in the ocean, t_f , can be either fixed or free (chosen to maximize J).

The fitness measure in equation (10) depends on both mortality and growth rates, and thus captures trade-offs between these two as a function of current and swimming velocity choices. Velocity decisions that increase growth can be seen as an investment in the future, whereby a larger size will confer a fitness advantage through higher future survival rate or higher fecundity. Velocity decisions that decrease mortality confer an immediate fitness advantage through higher survival rate. High growth and low mortality might be in conflict. For example, foraging movements might increase growth, but might also increase predation risk. At times optimal behaviours might favour higher growth over lower mortality or vice versa, so that in the end, fitness will be at a maximum.

SOLUTION OF THE OPTIMIZATION PROBLEM

Pontryagin's Maximum Principle

To solve the optimal control problem, I seek control variables, $u(t)$ and $v(t)$, and control parameter, t_f , that make fitness, J , as large as possible. This is accomplished using Pontryagin's Maximum Principle (PMP), where one first maximizes the appropriate Hamiltonian function and then solves a two-point boundary value problem (Pontryagin *et al.*, 1962).

For the fitness measure in equation (10) and the dynamics in equations (3) and (4), the relevant Hamiltonian (Lenhart and Workman, 2007) is

$$H(X, W, u, v, \lambda_1, \lambda_2, t) = -[u + v | \theta(X, t) k(X, W, t) - \mu_0(X, W, t) + \lambda_1(u + v) + \lambda_2 g(v, W, t)], \quad (11)$$

where λ_1 and λ_2 are additional unknown functions of t called the costate variables associated with the dynamics of displacement and weight, respectively.

Interpretation of the Hamiltonian and costate variables

To understand the ecological meaning of the Hamiltonian, one must first understand the meanings of the costate variables, which are tied to the fitness measure. The value function, $V(X, W, t)$, is the future fitness obtained by starting from a point (X, W, t) and proceeding optimally to the final time, t_f , where $X(t_f) = x_f$. Mathematically, this is expressed as

$$V(X, W, t) = \max_{u, v} - \int_0^{t_f} [u(\tau) + v(\tau) | \theta(X(\tau), \tau) k(X(\tau), W(\tau), \tau) + \mu_0(X(\tau), W(\tau), \tau)] d\tau + \Phi(W(t_f), t_f). \quad (12)$$

The costate variables $\lambda_1(t)$ and $\lambda_2(t)$ are the marginal contributions of the state variables $X(t)$ and $W(t)$, respectively, to value at time t :

$$\lambda_1(t) = V_X(X, W, t) \quad (13)$$

and

$$\lambda_2(t) = V_W(X, W, t), \quad (14)$$

where $V_X = \partial V / \partial X$ and $V_W = \partial V / \partial W$. I use this notational convention to represent partial derivatives throughout the paper. Note that since capture probability, k , decreases with weight, and terminal future reproductive success, Φ , increases with weight, $\lambda_2(t)$ must be positive (i.e. larger size confers a fitness advantage).

The elements of the Hamiltonian in equation (11) are then interpreted as follows: $|u + v| \theta k + \mu_0$ is the immediate rate of mortality; $\lambda_1(u + v)$ and $\lambda_2 g(v, W, t)$ are rates of change of value (future fitness) due to changes in downstream position and weight, respectively. Thus, the Hamiltonian weighs the trade-offs between immediate mortality and future rates of mortality and fecundity that are presented by alternative current velocity and swimming velocity choices.

The first step of the PMP is to maximize the Hamiltonian with respect to the control variables, u and v . This step of the PMP provides a suite of candidate optimal behaviours. When the Hamiltonian is maximized, it is equal to minus the marginal contribution of time to the value, namely

$$-V_t(X, W, t) = \max_{u, v} H(X, W, u, v, \lambda_1, \lambda_2, t). \quad (15)$$

Equation (15) is the Hamilton-Jacobi-Bellman equation (Bertsekas, 2017) and is derived using the principle of optimality, which states that the optimal control for the full problem, which starts at time t_0 , is also optimal for the problem starting at time $t_0 + \Delta t$, with initial states $X(t_0 + \Delta t)$ and $W(t_0 + \Delta t)$ (Lenhart and Workman, 2007).

Maximizing the Hamiltonian

I maximize the Hamiltonian graphically as a function of current velocity, u , and swimming velocity, v , in two steps. The first step is to maximize with respect to u along cross-sections

defined by fixed values of swimming velocity, v . The second step is to substitute this maximizing u (expressed as a function of v) into the Hamiltonian, then maximize this restricted Hamiltonian with respect to v .

For this first step, notice that any cross-section of the Hamiltonian defined by fixing v can be written as

$$H|_{v \text{ fixed}} = Y(u) + \text{constant}, \quad (16)$$

where

$$Y(u) = \begin{cases} \sigma_1(u + v) & \text{if } u \leq -v \\ \sigma_2(u + v) & \text{if } u > -v \end{cases} \quad (17)$$

and $\sigma_1 = \lambda_1 + \theta k$ and $\sigma_2 = \lambda_1 - \theta k$. Any u that maximizes $Y(u)$ also maximizes the Hamiltonian when v is fixed, and therefore, maximizing over cross-sections of the Hamiltonian is equivalent to maximizing $Y(u)$ with respect to u , such that $0 \leq u \leq u_{\max}$.

To maximize $Y(u)$, there are five cases to consider, each defined by the value of λ_1 relative to $-\theta k$ and θk ; namely, $\lambda_1 < -\theta k$, $\lambda_1 = -\theta k$, $-\theta k < \lambda_1 < \theta k$, $\lambda_1 = \theta k$, and $\lambda_1 > \theta k$. As λ_1 sweeps over values less than $-\theta k$ to values greater than θk , the linear pieces of $Y(u)$ rotate in unison, like minute hands of a clock, but in the counterclockwise direction. As these ‘minute hands’ rotate, their slopes change sign, which, in turn, changes the maximizing values of u . By considering each of the five cases for the position λ_1 and the current velocity domain $[0, u_{\max}]$ relative to the fixed value of $-v$, I characterize completely, the values of u that maximize $Y(u)$. The function $u^*(v)$ denotes the values of u that maximize $Y(u)$ for any given value of v (Figs. 3, 4).

In the second step of the maximization, I insert $u^*(v)$ into the Hamiltonian to make it a one-dimensional maximization problem in v . This restricted Hamiltonian is the sum of $\lambda_2 g(v)$ and a piecewise linear function, $L(v)$. By plotting these two functions on the same graph, I identify the maximizing swimming velocity, v^* , by inspection (Figs. 3, 4). As with $Y(u)$, the left and right linear pieces of $L(v)$ rotate counterclockwise as λ_1 moves from values less than $-\theta k$ to values greater than θk . And as before, the maximizing values of the Hamiltonian (using v this time instead of u) depend on the slopes of these ‘minute hands’, σ_1 and σ_2 . Inserting v^* into the function $u^*(v)$ yields the corresponding maximizing current velocity, u^* .

The canonical equations and the optimal control parameter

Thus far, I have identified the suite of optimal behaviours (by maximizing the Hamiltonian), but the trajectories of the optimal controls and state variables and the optimal control parameter, t_f^* , remain unknown. The canonical equations and transversality conditions supply the remaining information needed for a complete solution (Lenhart and Workman, 2007). The canonical equations are four ordinary differential equations that govern the dynamics of the costate and optimal state variables. The costate variables satisfy the differential equations

$$\frac{d\lambda_1}{dt} = -H_x^* \quad (18)$$

and

$$\frac{d\lambda_2}{dt} = -H_w^*, \quad (19)$$

where a subscript denotes partial differentiation. H_X^* is the function obtained by substituting the maximizing values of current and swimming velocities into the partial derivative of H with respect to X , and H_W^* is obtained by substituting the maximizing values of the current and swimming velocities into the partial derivative of H with respect to W . The optimal state variables satisfy the original state equations evaluated at u^* and v^* , namely

$$\frac{dX}{dt} = u^* + v^* \quad (20)$$

and

$$\frac{dW}{dt} = g|_{v=v^*}. \quad (21)$$

These four simultaneous differential equations require four boundary conditions. Three of the boundary conditions are given by $X(0) = 0$, $W(0) = w_0$, and $X(t_f) = x_f$. The remaining boundary condition is given by the transversality condition

$$\lambda_2(t_f) = \Phi_W|_{W=w(t_f)}. \quad (22)$$

This transversality condition follows from equation (14), which defines the weight costate variable at t_f : it is the marginal value of weight at the final time.

If the time of ocean arrival is free instead of fixed, a second transversality condition is used to determine the optimal control parameter, t_f^* :

$$(\Phi_{t_f} + H^*)|_{t_f=t_f^*} = 0. \quad (23)$$

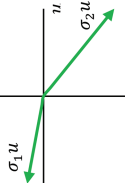
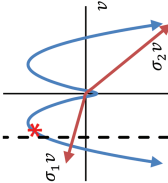
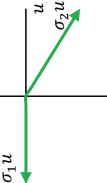
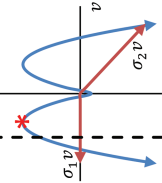
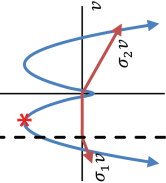
This equation follows from equation (15) (the Hamilton-Jacobi-Bellman equation) at the final time. There may, however, be several local optima for fitness as a function of the final time. Therefore, equation (23) may not uniquely determine an optimal time of ocean entry. In fact, there may be multiple times of entry with equal fitness.

The canonical equations along with their boundary conditions constitute a two-point boundary value problem, which can be solved numerically using the shooting method (Press *et al.*, 2007). The shooting method proceeds by using guesses at the initial conditions for λ_1 and λ_2 , then iteratively adjusting these until the final conditions are met, namely $X(t_f) = x_f$ and equation (22).

HANFORD REACH APPLICATION

The list of functions and parameter values used in the application of this model are summarized in Table A1 (see evolutionary-ecology.com/data/3233Appendix.pdf). I made a number of additional simplifying assumptions, beyond those of the general formulation. First, the final time, t_f , is time of arrival at the nearest downstream dam, McNary Dam (river km 470), not the time of ocean entry. Second, the objective measure is the logarithm of survival rate from emergence to adulthood. These simplifications were useful because there exist size-specific smolt-to-adult survival rate (*SAR*) estimates for fish released as juveniles recovered as adults at McNary Dam (Axel *et al.*, 2009). I used these estimates to define the terminal future reproductive success function, $\Phi(w)$, as $\log(\text{SAR})$.

In a sensitivity analysis, I allowed maximum current speed to vary between 0.05 to 2.5 m/s (converted to km/day). A maximum current velocity of 2.5 m/s was observed in the Hanford Reach of the Columbia River (Tiffan *et al.*, 2002). The length of residence time for salmon fry emerging in the Hanford Reach is largely unknown, but emergence occurs in the spring, and

Case	λ_1 condition	Plot of $\Upsilon(u)$	$u^*(v)$			Plot of $L(v)$ and $\lambda_2 g(v)$	Optimal velocities
1	$\lambda_1 < -\theta k$		$v < -u_{max}$	$-u_{max}$	0		RUM $u^* = 0$ $v^* = v' < -v_g$
2a	$\lambda_1 = -\theta k$		$[0, u_{max}]$	$[0, -v]$	0		AUM/SH $u^* \in [0, v_g]$ $v^* = -v_g$
3a	$-\theta k < \lambda_1 < \theta k$		u_{max}	$-v$	0		SH $u^* = v_g$ $v^* = -v_g$

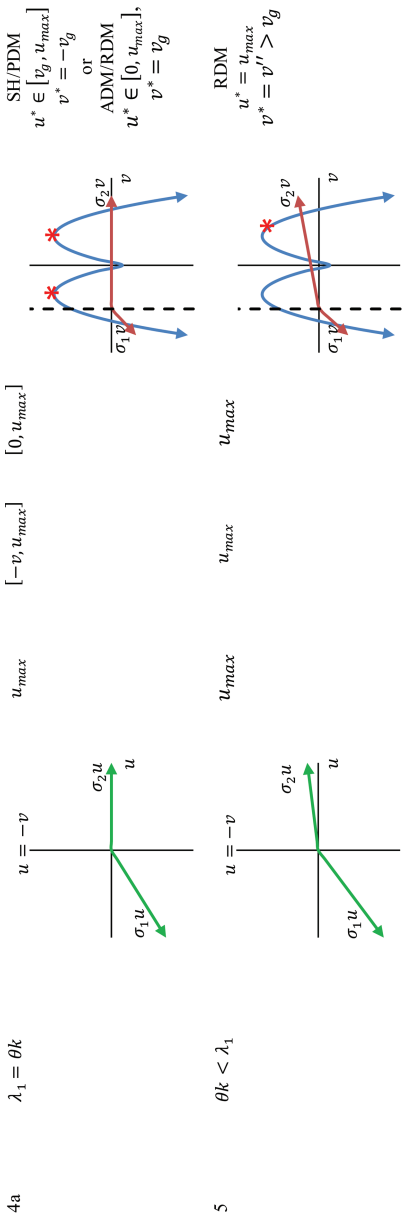


Fig. 3. Derivation of velocities that maximize the Hamiltonian, $H(v) = L(v) + \lambda_2 g(v)$, when $v \leq u_{max}$. Optimization is by inspection. The cases correspond to λ_1 conditions. $u^*(v)$, derived by examining the plot of $Y(u)$, gives the optimal choice(s) of current velocity for any given swimming velocity v . The slopes of the left-most and right-most linear pieces of $Y(u)$ and $L(v)$ are $\sigma_1 = \lambda_1 + \theta k$ and $\sigma_2 = \lambda_1 - \theta k$, respectively. The double-humped function, $\lambda_2 g(v)$, is symmetric about the vertical axis, $v = 0$, with maximums at $-v^g$ and v^g . The dashed vertical lines represent $v = -u_{max}^g$, and the asterisks mark the locations where the maximizing swimming velocities, v^* , intersect the growth curve. RUM = rapid upstream migration, ADM = appetitive upstream movement, SH = station holding, PDM = passive downstream migration, ADM = appetitive downstream movement, RDM = rapid downstream migration.

case	λ_1 and g_v condition	Plot of $Y(u)$	$\frac{u^*(v)}{v < -u_{max} \quad -u_{max} \leq v \leq 0 \quad 0 < v}$	Plot of L and $\lambda_2 g$	Optimal velocities
1	$\lambda_1 < -\theta k$		0		RUM $u^* = 0$ $v^* = v' < -v_g$
2b	$\lambda_1 = -\theta k$		$[0, u_{max}]$		AUM $u^* \in [0, u_{max}]$ $v^* = -v_g$
3b	$-\theta k < \lambda_1 < \lambda_1^{crit}$ $\sigma_1 + \lambda_2 g_v _{v=-u_{max}} < 0$		u_{max}		AUM $u^* = u_{max}$ $v^* = v'$
3c	$-\theta k < \lambda_1 < \lambda_1^{crit}$ $\sigma_1 + \lambda_2 g_v _{v=-u_{max}} \geq 0$		u_{max}		SH $u^* = u_{max}$ $v^* = -u_{max}$

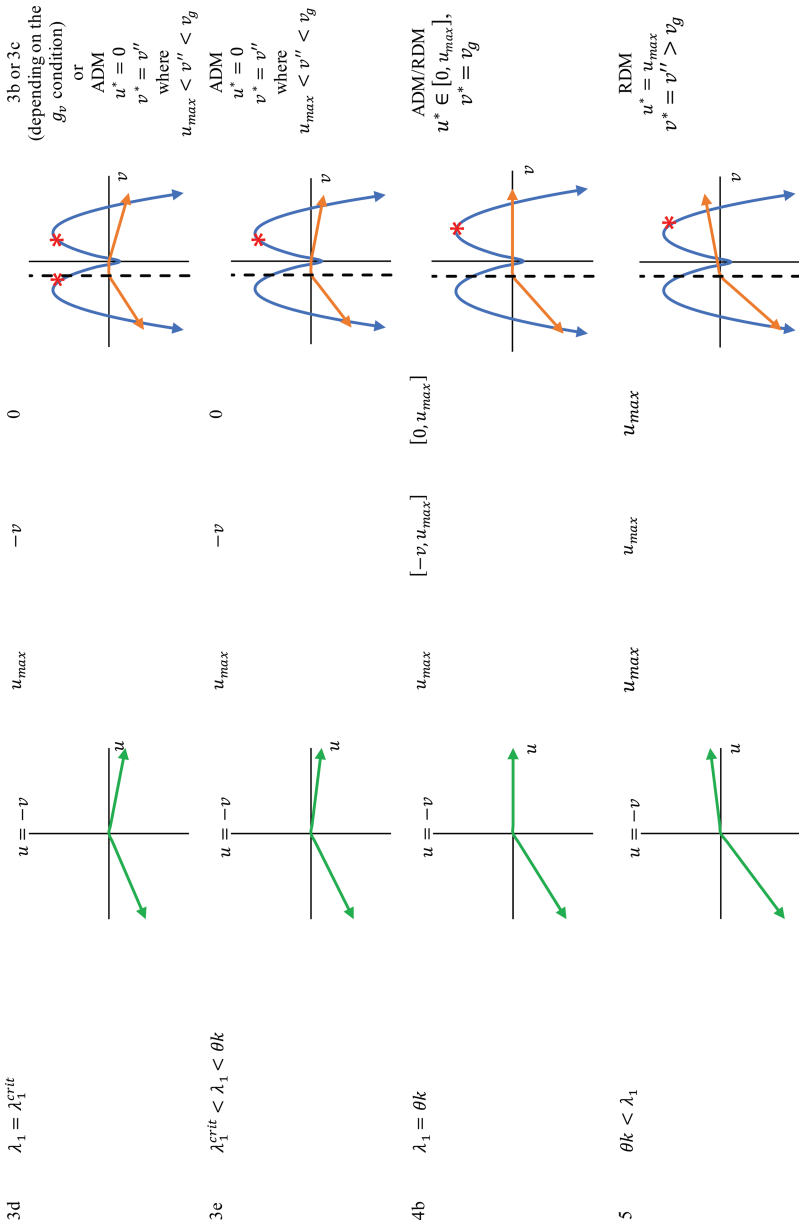


Fig. 4. Derivation of velocities that maximize the Hamiltonian, $H(v) = L(v) + \lambda_g g(v)$, when $u_{max} < v_g$. Optimization is by inspection. The cases correspond to the λ_1 and g_v conditions. Remaining figure elements are described in the legend to Fig. 3.

most fry have left the Hanford Reach on their seaward journey by July when temperatures become extreme (Becker, 1985). I set distance from the point of emergence in the Hanford Reach to McNary Dam at $X(t_p) = 135$ km, and times of emergence and arrival at McNary Dam to 4 March ($t_0 = 63$ days) and 3 April ($t_f = 93$ days), respectively.

I modelled growth using Holling's (1959) type II equation embedded in the Wisconsin Model of fish bioenergetics (Deslauriers *et al.*, 2017), so that

$$g(v, X, W, t) = \frac{C - R - SDA - FE - U}{E_2}, \quad (24)$$

where C (J/day) is consumption, R (J/day) is respiration, SDA (J/day) is specific dynamic action, FE (J/day) is egestion, and U (J/day) is excretion (Deslauriers *et al.*, 2017). E_2 (J/g) represents the energy density of a juvenile salmon, and is used to convert joules into grams.

Here consumption, as a function of time, weight, and swimming velocity is

$$C(v, W, t) = \frac{E_1 \alpha_0 v}{1 + \alpha_0 C_{\max}(W, t)^{-1} v}, \quad (25)$$

where E_1 (J/g) is energy density of prey, α_0 (g prey/km) is prey density, v (km/day) is swimming velocity, and $C_{\max}$ (g prey/day) is the maximum consumption rate. $C_{\max}$ is a function of weight and temperature that was derived for Chinook salmon (Deslauriers *et al.*, 2017). Respiration, R , and specific dynamic action, SDA , were also modelled using the functions for Chinook salmon (Deslauriers *et al.*, 2017). I modelled the costs of egestion and excretion as a fraction of consumption (Elliott, 1976). Both consumption and respiration rates depend on temperature. To model water temperature over the year, I fit a third degree trigonometric polynomial (Powell, 1981) to daily water temperature (in °C) data collected at Hanford Reach US Geological Survey (USGS) station gauges #12472900 (1974–1980) and #12472800 (1980–1993). I set weight at emergence to $w_0 = w(t_0) = 0.5$ g (Becker, 1973).

I assumed that mortality was due to predation alone, $\mu_0 = 0$, and capture probability was a function of juvenile salmon length and the length distribution of predators. If a prey (juvenile salmon) encountered a predator and the length of the prey was less than 46% of the length of the predator, then the prey was captured and killed (Pearsons and Fritts, 1999). I assumed a normal distribution for predator lengths and estimated the parameters from Gregory and Levings (1998) so that

$$k(W) = 1 - F\left(\frac{l(W) / 0.46 - 139.09}{42.09}\right), \quad (26)$$

where F is a cumulative normal distribution; $l(W)$ is a function developed by Becker (1973) that gives salmon length (mm) as a function of its weight (g); 139.09 (mm) and 42.09 (mm) are the mean and standard deviation, respectively, of the predator length distribution. The predator density, θ (predators per metre), was estimated by assuming a 5 g juvenile salmon has a survival rate of 0.40 over a distance of 135 km, which is roughly the survival rate from Hanford Reach to McNary Dam (Harnish *et al.*, 2014).

To solve the optimal control problem, I used packages available in the R programming language (R Core Team, 2020): (1) I computed numerical derivatives using the function *grad* in *numDeriv* (Gilbert and Varadhan, 2019). (2) I integrated the differential equations using *ode* in package *desolve* (Soetaert *et al.*, 2010). (3) I used the non-linear root-finding function *nleqslv* in package

nleqslv to find the initial conditions of the costate variables in the shooting method (Hasselman, 2018). (4) Finally, I maximized the Hamiltonian and freshwater growth function using the function *optimize*, which is a combination of golden section search and successive parabolic interpolation (Brent, 1973).

RESULTS

Optimal behaviours

In maximizing the Hamiltonian, I discovered a suite of five fundamental optimal behaviours (Fig. 5):

- Rapid upstream migration (RUM), in the slowest current swimming upstream at a speed that exceeds the swimming speed that maximizes growth.
- Appetitive upstream movement (AUM), which is a foraging movement distinct from migration (Southwood, 1962), in the swiftest current at a swimming speed that is less than the swimming speed that maximizes growth.
- Station holding (SH) against a current that is equal to the optimal growth speed. If maximum current velocity is less than the optimal growth speed, then station holding is against the current of maximum velocity, $u_{\max}$.
- Appetitive downstream movement (ADM), in the slowest current at a swimming velocity that is less than the swimming velocity that maximizes growth and greater than the maximum current velocity.
- Rapid downstream migration (RDM), in the swiftest current with a swimming velocity that exceeds the swimming velocity that maximizes growth.

Passive downstream migration, where a juvenile is carried downstream while swimming against the current (with a swimming velocity of $-v_g$) can also be optimal at the boundary $\lambda_1 = \theta k$ (Fig. 3). If $\lambda_1 = \theta k$ for more than an instant, then PDM could arise as an optimal behaviour.

The five fundamental optimal behaviours are functions of the marginal value of displacement, λ_1 and the maximum current velocity, $u_{\max}$. Where the values of these variables lie relative to four boundaries determines the optimal behaviour (Fig. 6). These boundaries are: $\lambda_1 = -\theta k$, $\lambda_1 = \theta k$, $\lambda_1 + \theta k + \lambda_2 g_{v|v=-u_{\max}} = 0$, and $\lambda_1 = \lambda_1^{\text{crit}}$. As Fig. 6 demonstrates, the boundaries $\lambda_1 = -\theta k$ and $\lambda_1 = \theta k$ distinguish between the foraging/predator avoidance behaviours (SH/AUM/ADM) and rapid migration (RUM and RDM). The boundary $\lambda_1 + \theta k + \lambda_2 g_{v|v=-u_{\max}} = 0$ distinguishes between SH and AUM, and $\lambda_1 = \lambda_1^{\text{crit}}$ distinguishes between SH/AUM and ADM.

Foraging/predator avoidance behaviour changes markedly with maximum current velocity. First, foraging/predator avoidance behaviours of station holding and appetitive movements are favoured if $|\lambda_1| < \theta k$. When maximum current velocity is greater than the swimming speed that maximizes growth, feeding/predator avoidance is station holding, with the juvenile selecting a current that matches the swimming speed that maximizes growth (Fig. 5a). This behaviour has the simultaneous advantages of minimizing predation risk while maximizing growth (i.e. there is no trade-off between foraging and predator avoidance). However, as maximum current velocity falls below the swimming velocity that maximizes growth, these simultaneous advantages disappear; instead, station holding in the current with maximum velocity or appetitive

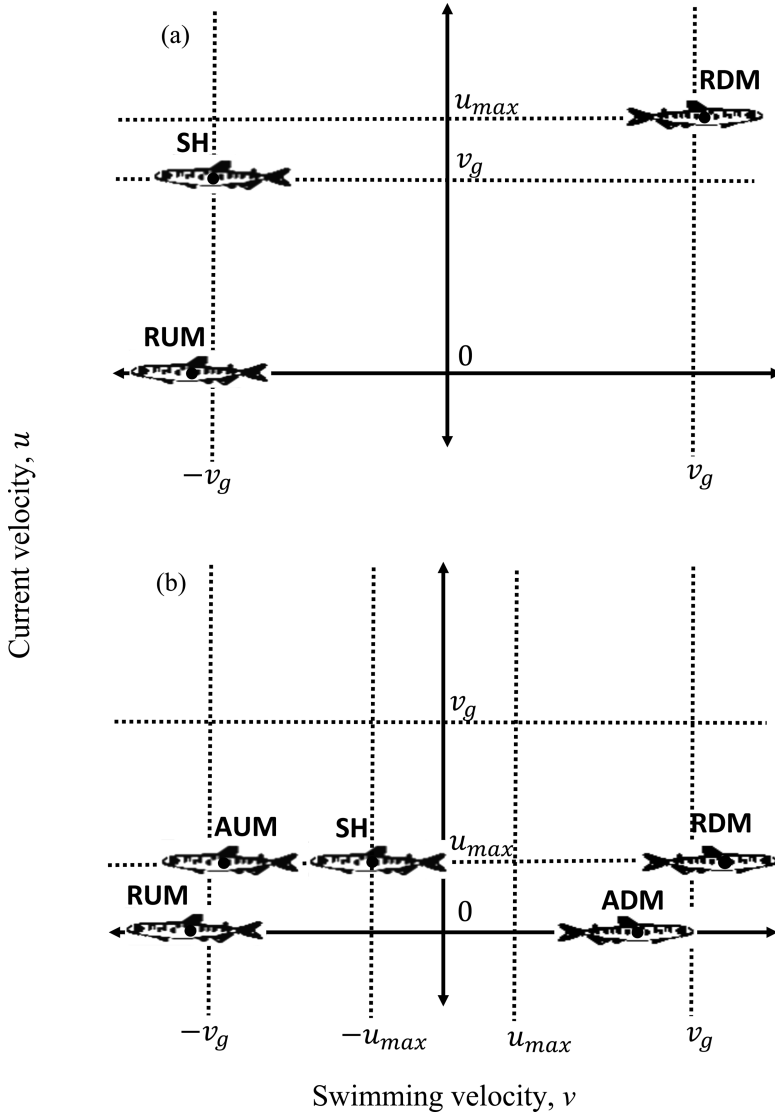


Fig. 5. The five fundamental optimal behaviours plotted in the u - v plane when: (a) $v_g < u_{max}$; (b) $u_{max} < v_g$. RUM = rapid upstream migration, AUM = appetitive upstream movement, SH = station holding, ADM = appetitive downstream movement, RDM = rapid downstream migration.

movement becomes optimal (Fig. 5b). Both of these behaviours yield less growth than station holding at a maximum growth speed. Furthermore, any appetitive movements increase predation risk beyond that of station holding. Therefore, when maximum current velocity decreases sufficiently, it reduces fitness in two ways: it lowers growth rate and increases predation risk.

A special case occurs when the swimming velocity that maximizes growth is zero. This happens, for example, with a drift feeder at night without sufficient light to recognize and

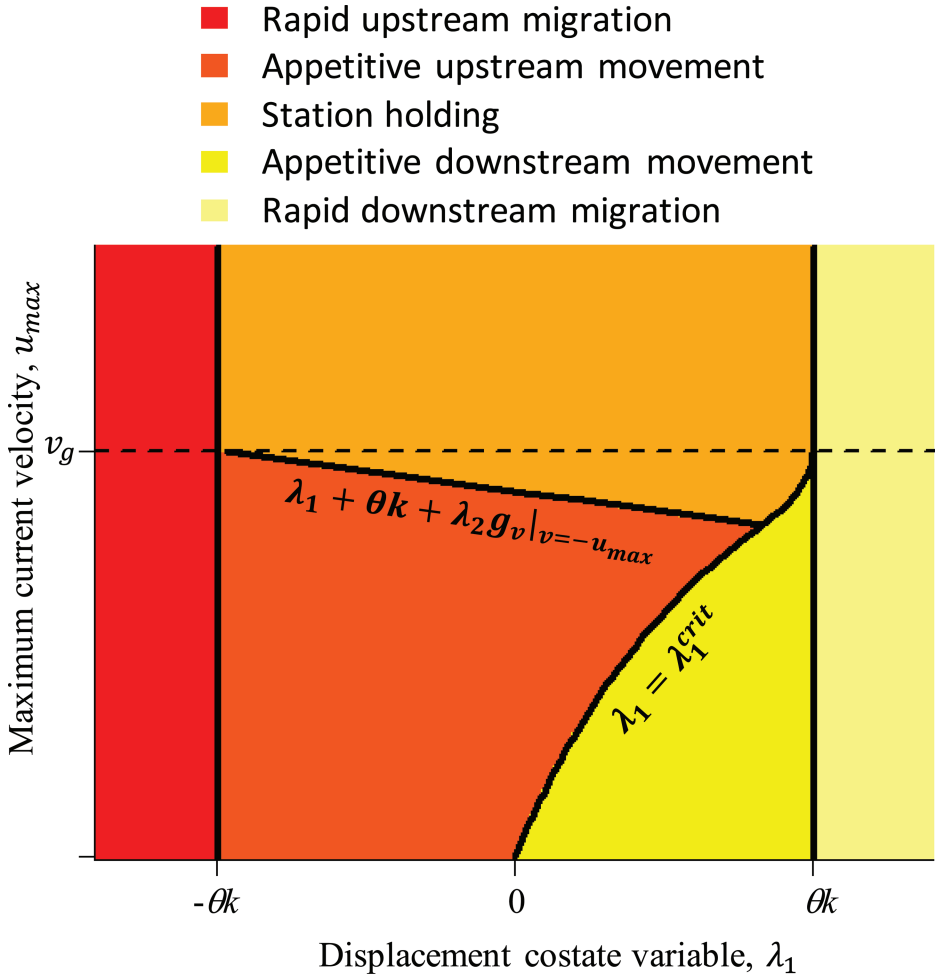


Fig. 6. The five fundamental optimal behaviours that arise in different locations of the λ_1 - u_{max} plane. The boundaries for the various behaviours are shown by the darkened curves that trace a path in the plane.

capture prey (Metcalfe *et al.*, 1997). Here, the growth rate function loses its double-hump form, and becomes a single-hump function centred at a swimming velocity of zero. Since $v_g = 0 < u_{max}$, the optimal behaviours are extracted from Fig. 3. These behaviours are SH with $v^* = u^* = 0$, which can be considered resting or settling; and either RUM or RDM, depending on the value of λ_1 .

Application to Hanford Reach

The complete results of the Hanford Reach application are in the supplementary materials (evolutionary-ecology.com/data/3233SupplementaryMaterial.xlsx), including trajectories of state and control variables reported every 0.1 days with maximum current velocities ranging from 0.05 to 2.5 m/s. Since the model is continuous in time, the variables could be reported at any desired

resolution, but I used 0.1 days to keep the size of the supplementary materials reasonable. Maximum current velocity strongly influenced the optimal behaviours (movement phases). When current velocity was sufficiently low (e.g. $u_{\max} = 0.24$ m/s), downstream movement was appetitive. (This illustrates that ‘appetitive movement’ can serve the dual purpose of foraging and migration.) For intermediate values of maximum current velocity (e.g. $u_{\max} = 0.42$ m/s), movement switched from station holding to downstream appetitive movement, followed by rapid downstream migration. When maximum current velocity was sufficiently high (e.g. $u_{\max} = 0.9$ m/s), movement switched directly from station holding to rapid downstream migration, with no appetitive movement in between. During downstream movement (appetitive or migratory), swimming accelerated as the juvenile salmon approached McNary Dam. Furthermore, the optimal onset of downstream movement occurred later as maximum current velocity increased (see supplementary materials).

Fish weight at McNary Dam and survival rate from emergence to adult both increase with maximum current velocity (Fig. 7). The greatest survival rate was realized when maximum current velocity was at 2.5 m/s, but there was little increase in weight or survival rate when maximum current velocity increased beyond $u_{\max} = 0.5$ m/s, indicating diminishing returns.

I checked this application for the possibility of a singular path which occurs when a switching function (σ_1 or σ_2) is zero for a span of time (Hestenes, 1966; Clark, 1990; Bertsekas, 2017). The Hanford Reach application does not have a singular path, because whenever a switching function is zero over a time interval, then, on this interval, $\dot{\lambda}_1 = -\theta k_w^* g^* = 0$ (if $\sigma_1 = 0$) or $\dot{\lambda}_1 = \theta k_w^* g^* = 0$ (if $\sigma_2 = 0$), since λ_1 is a constant (see equation 18). However, by choice of parameters and functions, $\theta > 0$, $k_w^* < 0$. Furthermore, $g^* > 0$, because whenever a switching function is zero, $|v^*| = v_g$ (Figs. 3, 4), and at this swimming speed, g is positive. Therefore, $\theta k_w^* g^* < 0$, which is a contradiction, and no singular path exists. Thus, the only behaviours predicted for the Hanford Reach application will be among the five fundamental behaviours.

DISCUSSION

Fundamental optimal behaviours vs. observations

The most general form of the optimality model predicts five fundamental optimal behaviours that are broadly categorized as ‘feeding and predator avoidance’ (appetitive upstream movement, station holding, appetitive downstream movement) and ‘rapid migration’ (rapid upstream migration, rapid downstream migration). The behaviour that is optimal at a given instant is determined by the magnitude of the marginal value of displacement, $|\lambda_1|$, relative to the marginal predation risk of displacement, θk , and maximum current velocity (Fig. 6). When the magnitude of the marginal value of displacement exceeds the marginal predation risk of displacement, rapid migration is optimal; otherwise, feeding and predator avoidance is optimal.

The form ‘feeding and predator avoidance’ takes depends critically on the maximum current velocity. I predict that station holding is the optimal feeding behaviour if the maximum current velocity is greater than the swimming speed that maximizes growth. In the Hanford Reach application, when maximum current velocity was sufficiently high during the station holding phase, maximum growth rate was achieved in increasingly rapid currents as the fish grew. This agrees with the observations that during rearing, juvenile salmonids move from low current velocity into midstream habitat with faster currents as they grow (Chapman and Bjornn, 1969; Lister and Genoe, 1970). When maximum current velocity is sufficiently low, the station holding feeding

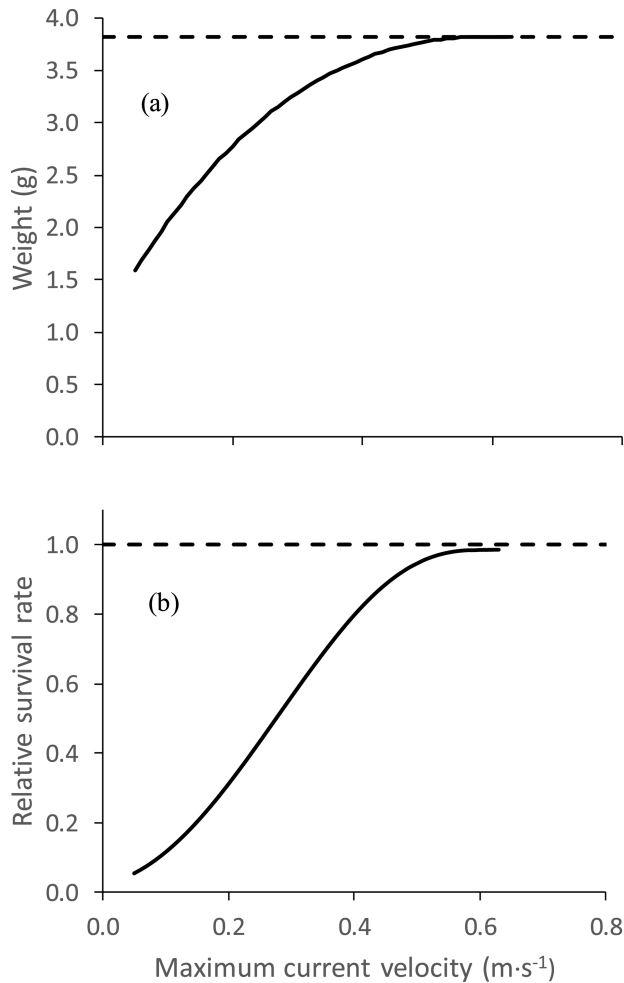


Fig. 7. (a) Weight of a juvenile fish upon arrival at McNary Dam and (b) relative survival rate from emergence to adult versus maximum current velocity. Relative survival rate is the survival rate divided by the survival rate at $u_{\text{max}} = 2.5$ m/s. The dashed lines represent horizontal asymptotes at 3.82 g and 1.0 in panels (a) and (b), respectively.

strategy becomes unprofitable because the food delivery rate is too low. In this case, the optimal strategy is to forage actively; this is the ‘nomad’ foraging strategy (Chapman, 1966; Nielsen, 1992).

The influence of maximum current velocity on the optimal feeding strategy suggests an explanation of feeding behaviours of lake-dwelling sockeye salmon (*O. nerka*) with near-zero current velocities (Burgner, 1991), and stream-dwelling coho salmon (*O. kisutch*) that feed in regions of rapid current velocity (Sandercock, 1991). Sockeye salmon that rear in lakes must actively seek out their prey (appetitive movement), while coho salmon in streams typically hold a territory while feeding (station holding), waiting for food to drift within striking distance (Nielsen, 1992).

Current velocity also influences the optimal migration behaviour. Fish can use high current velocities to reduce travel time during downstream migration to the ocean, reducing predation

risk in the migration corridor. Low current velocities favour appetitive downstream movement, while high current velocities favour rapid downstream migration. Whichever of these is optimal, the model, when applied to the Hanford Reach salmon population, predicts that fish will accelerate as they reach their destination. This prediction is consistent with tagging studies showing that juvenile salmon migration velocity increases as fish near the ocean, slowing just prior to entering saltwater (Carter *et al.*, 2009).

The two types of downstream movement predicted by the optimality model (appetitive movement and rapid downstream migration) describe the movements of two different races of Chinook salmon populations of the Columbia River: 'ocean-type' and 'stream-type' (Gilbert, 1913). Ocean-type juveniles migrate to the ocean within their first year of life and rear in the upper reaches of the mainstem Columbia and Snake rivers. Their migrations are protracted with little response to current velocity (Giorgi *et al.*, 1994), inhabiting segments of the river with low current velocities due to downstream dams (Raymond, 1979). Therefore, their downstream movements are best described as appetitive rather than migratory. Some individuals of the ocean-type race of Chinook salmon migrate long distances *upstream* (Giorgi *et al.*, 1994), possibly on foraging ventures (appetitive upstream movement).

In contrast, individuals of the 'stream-type' race migrate to the ocean after a year of rearing in upper tributaries (Gilbert, 1913). Stream-type populations can show rapid downstream migration that correlates positively with current velocity (Dauble *et al.*, 1989). Their downstream movements are more migratory than appetitive. For these stream-type individuals, the freshwater rearing stage, lasting over a year in upper tributaries, is followed by a rapid migration to the ocean.

Proposed experiment and study

My results on the influence of maximum current velocity on feeding strategy suggest an experiment in which one systematically varies the maximum current velocity from values above the swimming velocity that maximizes growth to values below, and observes whether the behaviour switches from 'sit-and-wait' to appetitive movement. This experiment could be carried out in an artificial stream channel (Dill and Fraser, 1984; Giannico and Healey, 1999; Piccolo *et al.*, 2008). Because predators are known to influence feeding and territorial behaviour (Metcalf *et al.*, 1987; Kim *et al.*, 2011), such an experiment should be conducted with and without the introduction of predators. In a related experiment, Fausch *et al.* (1997) found that some salmonids in experimental pools of a Japanese mountain stream responded to reduced drift by emigrating from pools. They also confirmed that salmonids shifted from ambush to active search mode when drift declined.

Observed current velocity choice allows us to determine whether upstream movements are best characterized as appetitive or migratory. That is, if fish swim in a slack current, movement is migratory; if fish swim in the most rapid current less than v_g , it is appetitive. If neither of these current velocity choices is observed, then the optimality model is missing a factor and needs to be improved. Sockeye salmon (*O. nerka*) populations are well suited to such a study since they sometimes move upstream from their natal stream to a lake to rear (Raleigh, 1967). Juvenile coho salmon (*O. kisutch*) and steelhead trout (*O. mykiss*) in Scott Creek, California also demonstrate upstream movements (Osterback *et al.*, 2018). Atlantic salmon (*Salmo salar*) juveniles may also exhibit this upstream migration pattern (Hutchings, 1986). Studies of movement can benefit greatly from the advancements in fish tagging and data collecting technologies for rivers and streams. Acoustic tags can track fine-scale movements of juvenile salmon (Wargo Rub *et al.*, 2020). In the Hanford Reach, Niehus *et al.* (2014) measured water velocity magnitude and direction using an acoustic Doppler current profiler and water level and temperature using a data logger.

Management implications

Changes to the flow regime of the Columbia River have influenced the current velocity choices available to salmon during their rearing and seaward migration. The optimality model shows that lowered current velocities can lead to reduced fitness and growth rate, change the relatively safe behaviour of station holding to more risky appetitive movements downstream, and slow the migration rate, increasing the mortality rate due to predation.

To mitigate for reduced flows, a Hanford Reach Fall Chinook Flow Protection Program Agreement (HRCFPPA) was established to control flow fluctuations and levels throughout the Hanford Reach for the protection of spawners, redds, and rearing fry (Langshaw *et al.*, 2018). To help endangered and threatened populations persist in the Columbia Basin, water is released from storage reservoirs to increase flows for salmon and steelhead (National Oceanic and Atmospheric Administration, 2020).

Results from the optimal control model suggest that flows should be managed so that maximum current velocity does not fall below the swimming speed that maximizes growth; otherwise, station holding will become less profitable, leading to a reduction in both growth and survival rates of juvenile salmon in the Columbia Basin.

CONCLUSIONS

A dynamic optimality model proved useful for understanding juvenile anadromous salmonid movements. Solving the optimality model revealed five optimal behaviours or movement phases, roughly categorized as ‘feeding/predator avoidance’ and ‘rapid migration’, and identified the conditions that determine which behaviour is optimal at any instant. Results from the optimality model suggest an experiment to determine how foraging behaviour changes with maximum current velocity in an experimental stream, and a study to investigate whether upstream movement of juvenile salmonids is appetitive or migratory. Existing data allow only a caricature of the selective forces at play, but as fine-scale movement and river data are gathered using improved technologies, the optimality model can be tested and refined, allowing us to better grasp why juvenile salmonids behave as they do.

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