

Facultative anadromy in salmonids: linking habitat, individual life history decisions, and population-level consequences

Steven F. Railsback, Bret C. Harvey, and Jason L. White

Abstract: Modeling and management of facultative anadromous salmonids is complicated by their ability to select anadromous or resident life histories. Conventional theory for this behavior assumes individuals select the strategy offering highest expected reproductive success but does not predict how population-level consequences such as a stream's smolt production emerge from the anadromy decision and habitat conditions. Our individual-based population model represents juvenile growth, survival, and anadromy decisions as outcomes of habitat and competition. In simulation experiments that varied stream growth and survival conditions, we examined how many simulated juveniles selected anadromy versus residence and how many of those choosing anadromy survived until smolting. Owing to variation in habitat and among individuals, the within-population frequency of anadromy changed gradually with growth and survival conditions instead of switching abruptly. Higher predation risk caused more juveniles to select anadromy, but fewer survived long enough to smolt. Improving growth appears a much safer way to increase smolt production compared with reducing freshwater survival. Smolt production peaked at high growth and moderately high survival, conditions that also produced many residents.

Résumé : La modélisation et la gestion de salmonidés à anadromie facultative sont compliquées par la capacité de ces poissons de choisir un cycle biologique soit anadrome ou résident. La théorie classique en ce qui concerne ce comportement repose sur le principe que les individus choisissent la stratégie qui leur permettrait le plus grand succès de reproduction, mais elle ne prédit pas comment les conséquences à l'échelle de la population, comme la production de saumoneaux dans un cours d'eau donné, découlent de la décision relative à l'anadromie et des conditions de l'habitat. Notre modèle de population basé sur les individus représente la croissance, la survie et les décisions relatives à l'anadromie de poissons juvéniles en tant que résultats de l'habitat et de la concurrence. Dans des expériences de simulation dans lesquelles variaient les conditions de croissance et de survie en rivière, nous avons examiné le nombre de juvéniles simulés qui choisissait l'anadromie, d'une part, et la résidence, d'autre part, et de ceux qui choisissaient l'anadromie, le nombre qui survivait jusqu'à la smoltification. En raison des variations d'habitat et entre individus, la fréquence d'anadromie au sein d'une population donnée variait graduellement, plutôt qu'abruptement, en réponse aux variations des conditions de croissance et de survie. Un risque de prédation accru portait plus de juvéniles à choisir l'anadromie, même si un plus petit nombre survivaient jusqu'à la smoltification. L'amélioration de la croissance semble être une manière beaucoup plus sûre d'accroître la production de saumoneaux que la réduction de la survie en eau douce. La production de saumoneaux atteignait un maximum quand la croissance était élevée et la survie, modérément élevée, des conditions qui produisaient également de nombreux résidents. [Traduit par la Rédaction]

Introduction

Predicting effects of management actions on facultative anadromous salmonids is important yet notoriously difficult. These species (e.g., rainbow-steelhead trout (*Oncorhynchus mykiss*), brown-sea trout (*Salmo trutta*), Atlantic salmon (*Salmo salar*)) are now understood to include individuals that migrate to the ocean and others that remain resident in fresh water, with the adaptive decision of whether and when to migrate to the ocean based (at least in part) on individual state and history (Mangel 1994; Metcalfe 1998). Many populations with such variable life histories are endangered or otherwise of high management importance and the target of costly management programs, often focused on preserving the anadromous life history.

However, facultative anadromy (often referred to as “partial migration”; Secor and Kerr 2009) itself makes predicting the effects of management difficult. If, for example, we restore stream flows, temperatures, and physical habitat to improve survival and growth of juveniles in their natal stream, will we produce more anadromous fish? Or will these habitat improvements cause more

fish to remain as residents and produce fewer anadromous individuals?

These questions have long been of interest and have been examined from several perspectives. For example, Jonsson and Jonsson (1993) discuss anadromy and its relation to growth, sex, habitat, and reproductive strategy. Schaffer (2004) and Hendry et al. (2004) look at anadromy largely from a life history and evolutionary perspective. The role of physiology (especially metabolic rate) in explaining anadromy has been examined by Forseth et al. (1999), Morinville and Rasmussen (2003), and Sloat and Reeves (2014).

Here, we focus on the perspective of anadromy (the individual choice of whether and when to smolt and migrate to the ocean) as an adaptive behavior. This perspective (e.g., Metcalfe et al. 1988; Metcalfe 1998; Grand 1999; Mangel and Satterthwaite 2008) has led to an established theoretical framework, which assumes that individual life history decisions (i) are made to maximize expected future reproductive success, which depends on both survival to and size at spawning; (ii) are made in advance of their implementation (e.g., a juvenile decides to smolt in the spring and actually

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S.F. Railsback. Lang Railsback & Associates, 250 California Avenue, Arcata, CA 95521, USA.

B.C. Harvey and J.L. White. USDA Forest Service, Pacific Southwest Research Station, 1700 Bayview Drive, Arcata, CA 95521, USA.

Corresponding author: Steven F. Railsback (e-mail: Steve@LangRailsback.com).

smolts and migrates out to the ocean the following fall); (iii) are based in part on an individual's current size, growth rate, and mortality risk; and (iv) affect behavior between the time they are made and when they are implemented (e.g., by causing fish that have decided to smolt to feed more and grow more rapidly).

This theoretical framework has recently been applied to *O. mykiss* at sites including California coastal streams and Central Valley rivers (Satterthwaite et al. 2009, 2010; Sogard et al. 2012) and a stream in Washington (Benjamin et al. 2013). These studies modeled whether an individual fish should smolt and become anadromous versus remain resident, as a consequence of its current age and size and the growth and survival rates it anticipates for the freshwater and ocean alternatives. Life history transformations such as smolting and outmigration were assumed to occur on specific dates, and mathematical optimization was used to determine whether a female salmonid's lifetime egg production is maximized by remaining a resident or becoming anadromous at one of several potential ages. These studies are very useful for understanding factors that could promote anadromy and successfully reproduced observed patterns in anadromy.

Modeling how individuals select anadromy, however, does not by itself predict how management actions affect populations of facultative anadromous fish. First, modeling how the anadromy decision depends on survival and growth conditions also requires predicting how management actions such as restoring flows, temperatures, and habitat complexity affect survival and growth. Second, these models do not consider competition and other feedbacks of individual behavior; if, for example, more individuals decide to smolt and migrate out of a stream, does the resulting decrease in competition for stream food and feeding habitat affect the growth and survival and therefore the anadromy behavior of other individuals (Vincenzi et al. 2012)? (Or, in contrast, if fewer individuals decide to smolt, does increased stream abundance encourage later-emerging individuals to smolt?) Third, the individual behavior models do not predict population-level responses such as the abundance of residents and the production of smolts; these models may predict whether juveniles are anadromous or resident in a particular situation but not whether management actions would increase or decrease their numbers.

We describe and explore a model that fills these gaps and relates production of resident and anadromous forms of facultative anadromous salmonids to stream management. The model implements the same basic framework for anadromy behavior within an individual-based population model that represents how habitat and competition affect growth and survival of juvenile salmonids. Whereas the models of Satterthwaite et al. (2009, 2010) predict the optimal anadromy decision of an individual, given its size, growth, and survival probability, our model simulates a population of individuals, each with its own size, growth, and survival emerging from dynamic habitat conditions and competition; how each individual decides whether to become anadromous; and the resulting population-level production of smolts and residents. We apply the model to a chain of study sites on a stream in California's Central Valley and examine how predicted numbers of anadromous and resident *O. mykiss* vary with growth and survival conditions. To keep this first analysis of the model tractable, we do not yet explore its ability to predict effects of management factors such as flow and temperature regime and channel restoration. Like Satterthwaite et al. (2010), we analyze our model's sensitivity to key parameters to make inferences about important processes and identify knowledge gaps. Even though we apply the model to a real study site, our objective here is not to make or test site-specific predictions but to understand the model and what it tells us about general responses of facultative anadromous popu-

lations to management actions and ecological context, in an environment closer to nature in complexity.

Materials and methods

The model: inSALMO-FA

We modified an existing individual-based model of freshwater life stages of salmon (inSALMO; Rallsback et al. 2013) to include facultative anadromy as an additional behavior, by adapting the theory of Satterthwaite et al. (2009, 2010). The resulting model, termed inSALMO-FA, is one of a family of stream salmonid models for research and management applications (e.g., Rallsback and Harvey 2001, 2002; Rallsback et al. 2005, 2009; Harvey and Rallsback 2014). A detailed description of inSALMO-FA is provided in the online Supplementary Material¹; here, we summarize the model with focus on the anadromy behavior. To summarize the model's conceptual design, Table 1 describes how a standard set of individual-based modeling design concepts (Grimm et al. 2010) are implemented.

The purpose of inSALMO-FA is to help predict and understand how river management actions such as altered flow and temperature regimes and habitat restoration projects affect the spawning and juvenile rearing life stages — especially smolt production — of facultative anadromous salmonids. The model simulates how individual fish interact with the stream environment and each other to determine their survival and growth and how population characteristics emerge from the fate of individuals. Because the model's purpose is limited to freshwater habitat management, many complexities of facultative anadromous life cycles (e.g., iteroparity, early maturing males) are neglected. The model was developed for steelhead (*O. mykiss*) management in California but is designed for application to other streams, regions, and facultative or obligate anadromous salmonid species. (Modeling populations that do not meet the simplifying assumptions of our anadromy theory, below, would require modifications.)

The model represents freshwater life stages of facultative anadromous salmonids (and, optionally, obligate anadromous salmon such as other *Oncorhynchus* species): from adults arriving in spawning streams, to spawning, egg incubation, emergence, juvenile rearing, and outmigration. It operates at a 1-day time step and can simulate one or a sequence of years. Habitat is represented as one or more stream reaches, each typically a few hundreds to thousands of metres in length. Reaches have variables for daily flow, temperature, and turbidity. While food availability, growth, and predation risk depend on characteristics of fish and habitat cells as described below, reaches also have constant parameters controlling the overall magnitude of food availability (drift food concentration; production of benthic food) and predation risk (daily survival of fish and terrestrial predators in the most risky habitat). Each reach is made up of habitat cells; cells are irregular polygons laid out to capture essential habitat variability while being no smaller than the area used by typical fish. Cells are typically one to tens of square metres in area, with hundreds to a few thousands of cells per reach. Cells have flow-dependent variables for depth, velocity, and daily food availability, plus static variables representing availability of spawning gravel, velocity shelter for drift feeding, and hiding cover. Predation risk depends on several variables of a fish and its cell, and risk due to terrestrial animals (birds, otters, etc.) is represented separately from risk due to larger fish.

Adult salmonids are represented as individuals with variables for species, sex, length, and mass. Upon spawning, adults create redds, which have variables for the number of viable eggs and their developmental status. For computational tractability, juve-

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2014-0091>.

Table 1. Summary of how inSALMO-FA implements the individual-based modeling design concepts of Grimm et al. (2010).

Concept	Implementation for juvenile <i>O. mykiss</i> in inSALMO-FA
Basic principles	Anadromy is modeled as an adaptive behavior based on experienced growth and survival, not genetic or physiological processes.
Emergence	Primary results (number of smolts and nonanadromous juveniles) emerge from habitat availability, the number of spawners, and adaptive behavior of juveniles.
Adaptation	Juveniles have two adaptive behaviors: habitat selection (each day, selecting a feeding cell or deciding to move downstream) and anadromy (deciding whether to prepare for smolting).
Objectives	Habitat selection is modeled by assuming juveniles select the cell that maximizes an objective that trades off growth versus predation risk (Railsback et al. 1999; the exact measure differs among life history stages). The objective of anadromy behavior is to maximize expected offspring at the next spawning opportunity.
Prediction	Habitat selection uses the prediction that growth and survival conditions on the current day will persist over a decision time horizon (which differs among life history stages). Anadromy uses memory over the past 30 days as the predicted growth and survival probability for time remaining in the stream.
Sensing	In selecting habitat, juveniles are assumed to sense and potentially move to cells within a radius that increases with fish length and always contains the adjacent cells. The memory used in the anadromy decision contains the actual daily growth the individual obtained, and the survival probability it was exposed to, in the cells it occupied on the previous 30 days. Expected survival and growth for anadromy are constant parameters that juveniles “know” the value of.
Interaction	Juveniles interact with each other indirectly, via size-based competition for two resources: the food and the area of velocity shelter for drift feeding in each cell. Food and shelter used by one fish are not available to any smaller fish.
Stochasticity	There is little randomness in juvenile simulations. Whether each fish dies each day is stochastic, but the probability of survival is a deterministic function of the fish and its habitat cell. When juveniles move downstream, they are placed in a cell selected randomly from those with moderate velocity in the next downstream reach.

niles are represented as “superindividuals”: simulation objects that each represent (in this study) 10 individual fish. Juveniles have variables for sex, length, mass, and life history status. This status is set to “juvenile” at emergence; if a juvenile commits to anadromy, its status is changed to “presmolt” until it begins downstream migration, when its status is changed to “smolt”. If a juvenile instead commits to spawning as a resident, its status is set to “prespawner”.

On each simulated day, the model executes a fixed schedule of actions. (1) Habitat is updated by reading in the daily flow, temperature, and turbidity of each reach; cells then update their flow-dependent variables. (2) Any adults scheduled to “arrive” from the ocean are created and placed in their spawning reach. (3) Any female adults that are ready to spawn select a cell, create a redd in it, and (along with a nearby male) incur a mass loss that typically causes them to die soon (the fate of spawned adults is unimportant for this model). (4) All fish select habitat, with the habitat selection objective varying among life stages; adults select a cell that maximizes their survival, while fish in the pre-adult life stages select a cell to maximize their expected future reproductive output (explained further below). The radius within which fish select a cell increases with their length but always includes at least the adjacent cells. During an initial period after emergence, juveniles can alternatively choose “outmigration” — movement to the next downstream reach or out of the model — if expected future reproductive output in their current reach is very low. (This early outmigration is typically executed by newly emerged juveniles that fail to find productive rearing habitat, reproducing the high emigration of newly hatched fry observed at our study site (Railsback et al. 2013).) Habitat selection is executed in order of fish length to represent a size-based hierarchy; larger fish get first access to food and preferred habitat. (5) Fish grow according to the food intake and energy costs experienced in their cell. (6) All fish are subjected to mortality risk from several sources (especially terrestrial and fish predators, as well as starvation–disease); the probability of each kind of mortality depends on characteristics of the individual fish and their habitat cell. (7) Non-adult fish update their life history status (as explained below); juveniles decide whether to become presmolts, become prespawners, or remain uncommitted, and presmolts decide whether to smolt and begin downstream migration. (8) Redds are subjected to mortality; some

or all eggs in each redd can die from causes such as dewatering, scour, and extreme temperature. (9) The development status of each redd is updated by a temperature-dependent amount. (10) For fully developed redds, eggs become new juvenile fish. (11) Model outputs are updated.

We implemented inSALMO-FA by modifying the software for inSALMO (Railsback et al. 2013), which was modified from the software for inSTREAM (Railsback et al. 2009). We tested the software using spot checks and visual evaluation using the graphical displays, statistical analysis of output files for anomalous results, and completely reimplementing all major submodels and testing them against inSALMO’s many optional output files. For example, we tested the behavioral theory added to inSALMO-FA by writing out the state of each juvenile on each day and the results of its life history decisions and comparing these results against an independent implementation of the theory in spreadsheet software.

Anadromy theory

To model how individual juveniles decide whether to become anadromous or remain resident, we adapted the approach of Satterthwaite et al. (2009, 2010) to the more complex context of inSALMO. Our adaptation (fully explained below) required three modifications. First, we considered only two life history options: smolting and migrating to the ocean within the first year after emergence or remaining as a resident intending to spawn at age 2. Satterthwaite et al. (2010) found these two options the most commonly chosen in both model predictions and observations from two Central Valley rivers. Second, because mathematical optimization of life history is not feasible in a population of competing individuals, we used “state- and prediction-based” theory (Railsback and Harvey 2013), by assuming individuals predict future survival and growth from their recent experience and use the predictions to estimate expected fitness under each option. Third, we neglected multiple spawning in modeling expected fitness.

These modifications eliminated the need for several assumptions made by Satterthwaite et al. (2009, 2010). Most importantly, we did not need to impose a fixed timeline of dates for life history events; instead, we allowed uncommitted juveniles to reconsider anadromy every day over an extended period. At our study site, steelhead adults appear to spawn over an extended period — we assumed December through April — and smolt counts in an out-

Table 2. Anadromy behavior parameter definitions, values, and bases.

Parameter	Meaning	Value	Basis
Memory list length	Number of days over which fish “remember” growth and survival, and number of days after emergence before juveniles start making anadromy decisions	30 days	Estimate, long enough to smooth short-term events but short enough to capture seasonality
Spawning start date	First date of spawning	1 January	Estimate from field observations
Maturity decision interval	Minimum time between commitment to residency and spawning	180 days	Thorpe et al. 1998
Smolt delay (D)	Time between decision to smolt and start of downstream migration	120 days	Value used by Satterthwaite et al. (2010) for sites with long migration to ocean
Maximum ocean survival ($S_{O-\max}$)	Maximum probability of surviving from outmigration to adulthood	0.02	Review of steelhead survival estimates
Ocean survival 10% length, 90% length	Length at which expected ocean survival is 10%, 90% of maximum	15 cm (10%), 20 cm (90%)	Review of steelhead survival estimates
Expected offspring for anadromous females, males	Expected number of offspring (e.g., fertilized eggs) for anadromous females, males	7100 (females), 3500 (males)	Satterthwaite et al. (2009) for females; reduced by half for males to reflect lower benefit of anadromy

migrant trap indicate no clear seasonal peak (though these counts are very low), indicating considerable flexibility in the timing of outmigration (Earley et al. 2008). The use of only two life history options also allowed us to model males in the same way we model females (Satterthwaite et al. (2009, 2010) ignored males), while recognizing that this simplification is less valid for males (Sloat et al. 2014).

Juveniles in inSALMO-FA make no life history decisions until their age (in days) reaches the value of a parameter for memory list length (explained further below and in Table 2). This is the same period during which juveniles can migrate downstream as non-smolts if their expected survival is very low.

After this initial period, remaining juveniles decide each day whether to turn into a presmolt, irreversibly becoming anadromous. If a juvenile has not become a presmolt by a date representing the time at which commitment to resident spawning must be made, it becomes a prespawner that intends to spawn as a resident the following spawning season. This date of commitment to resident spawning is set by a parameter for the maturity decision interval; a fish can no longer choose anadromy if the number of days between the current date and the start of the next spawning season (which is set by another parameter; Table 2) exceeds the maturity decision interval. The time between when a juvenile becomes a presmolt and when it begins downstream migration is set by the smolt delay parameter.

From emergence, juveniles maintain “memory” of growth and survival: lists of their length and survival probability (for risks other than starvation; mainly predation but potentially also high temperature and extreme velocity) for each day. The length of these lists (number of previous days remembered) is the value of the memory list length parameter.

The decision of whether to become a presmolt is made by comparing expected fitness from anadromy (F_A) to expected fitness from residence (F_R); if F_A is greater than F_R then the juvenile becomes a presmolt. As in the model of Satterthwaite et al. (2010), F_A and F_R represent expected numbers of future offspring, the product of expected probability of surviving to reproduction and estimated number of offspring (eggs produced or fertilized).

For anadromy, $F_A = S_S \times S_O \times O_O$. S_S is expected survival to smolting, the product of two components, survival of starvation and non-starvation risks, S_O is expected survival through the ocean life stage, from smolt outmigration through return to fresh water as an adult, and O_O is the expected number of offspring for anadromy. Survival of risks other than starvation is calculated as $(S_M)^D$, where S_M is the mean of the daily survival probabilities on the memory list, and D is the smolt delay parameter. Survival of starvation is $(\bar{S})^D$, where $\bar{S}$ is the mean starvation survival (eq. 2 of

Rallsback et al. 1999), a function of the fish’s current condition and growth rate. Growth is assumed to continue at the mean rate over the fish’s growth memory.

Following Satterthwaite et al. (2010), we modeled S_O as a logistic function of the length (L_S) at which smolts migrate downstream: $S_O = S_{O-\max} \times \text{logistic}(L_S)$. $S_{O-\max}$ is a parameter for maximum survival of the ocean life stage, and L_S is calculated by multiplying the mean growth rate over the memory period by D and adding that increment to the fish’s current length. The logistic function of L_S is defined by parameters (L_1 , L_9) defining the lengths at which survival is 0.1 and 0.9 of maximum, respectively:

$$\text{logistic}(L_S) = \frac{\exp(Z)}{1 + \exp(Z)}$$

$$\text{where } Z = \ln(1/9) + \left[\left(\frac{\ln(81)}{L_1 - L_9} \right) (L_1 - L) \right]$$

This model of survival from outmigration through adult return embodies assumptions that turn out to be important to our conclusions: risk during that period is dominated by size-dependent predation before the fish reaches adult size, and survival is therefore independent of the time adults spend in the ocean.

The expected number of offspring for anadromy O_O is assumed constant, with separate values for females and males (set by parameters; Table 2). A lower value of O_O is used to impose a lower overall benefit of anadromy on males.

Because of our simplification that residents spawn at age 2, expected fitness for remaining a resident F_R is approximated as expected reproductive output at age 2. F_R is the product of expected survival to age 2 spawning (S_2) and the expected number of offspring at age 2 spawning (O_2). S_2 is calculated like S_S , except that instead of D , the time horizon is the number of days until the first day of spawning in the year when the fish is age 2. The value of O_2 is calculated using inSALMO’s equation and parameters for fecundity: for *O. mykiss*, $O_2 = 0.11(L_2)^{2.54}$. L_2 is the expected fork length at age 2 spawning, projected from current length and the mean growth rate over the fish’s memory. Males receive the same value of O_2 as females.

Effects of life history on habitat selection behavior

The effect of fish length on expected ocean survival gives juveniles selecting the anadromous life history a strong incentive to grow, and growth acceleration has been observed in real presmolts (Metcalf et al. 1988). In contrast, fitness of residents is less size-dependent and therefore more likely to be maximized by avoiding unnecessary risk. Hence, inSALMO-FA assumes different

habitat selection objectives — the trade-offs between growth and predation risk made when selecting a cell for feeding — for the different life history alternatives. Juveniles that have not yet committed to either anadromy or resident spawning select cells to maximize the “expected reproductive maturity” fitness measure of Rallsback et al. (1999). This measure represents expected survival of both starvation and predation risk over a 90-day future time horizon and how close to reproductive size the individual would be at the end of the horizon.

Presmolts select the habitat cell with highest value of a fitness measure equivalent to F_A , except that S_S is evaluated for a cell using the growth and survival available at the cell instead of from the fish's memory, and the time horizon is the number of days remaining until downstream migration begins instead of D . Once a smolt begins downstream migration, it moves downstream one reach per day and then selects a cell using the same measure as presmolts (or is recorded as an outmigrant and removed when leaving the most downstream reach).

Prespawners select habitat to maximize a fitness measure equivalent to F_R , except that cell-specific values of growth and survival are used instead of the fish's memory.

Study site and model input

We applied inSALMO-FA to *O. mykiss* in lower Clear Creek, from Whiskeytown Reservoir to its confluence with the Sacramento River, Shasta County, California. Clear Creek has been intensively studied and managed as a highly productive spawning stream for Chinook salmon (*Oncorhynchus tshawytscha*); the reservoir provides moderate flows and temperatures year-round, and restoration projects have provided extensive spawning gravel and improved hydraulic habitat (Rallsback et al. 2013; Gard 2014). Conservation of steelhead is also an important objective, so managers are concerned about whether enhancement for Chinook salmon encourages or discourages anadromy in *O. mykiss*.

Model input was developed from hydraulic models and habitat data developed by the US Fish and Wildlife Service (e.g., Gard 2006, 2014) to capture and represent habitat throughout lower Clear Creek. We simulated a sequence of 17 sites (containing 13 282 habitat cells) that include five in the steeper upstream section where steelhead dominate and 12 in the alluvial section downstream where spawning is dominated by Chinook salmon. The 17 simulated reaches represent a total of 4953 m length, 17% of the 29 300 m total length of Clear Creek below the reservoir.

Even though fall-run Chinook salmon are more abundant than steelhead at the study sites and inSALMO-FA can simulate both species in sympatry (with individuals of both species competing for habitat and food), we chose to simulate only *O. mykiss*. This decision was made to reduce computational effort, but only after a pilot analysis showed very little effect of Chinook on simulated *O. mykiss*. This lack of effect was because fall Chinook spawn and emerge much earlier than *O. mykiss*, and at our site very few Chinook juveniles remain in their natal streams long enough to compete with *O. mykiss*.

Our simulation experiments modeled 6 years, 2006–2011, but with no spawning in 2011 because juveniles born that year would not have time to decide between anadromy and residence. These years included a wide range of spawner densities, from 1 to 14 spawning females per kilometre. The simulated number of spawners in each site for each year was derived from the annual count of steelhead redds in all of lower Clear Creek estimated by Giovannetti et al. (2013). We (i) multiplied this total redd count by site length divided by total stream length, (ii) multiplied by two to represent males as well as females, and (iii) used a minimum of at least three spawners per site per year to make it likely that at least one female occurred. The resulting numbers of spawners were initialized each simulated year, with the arrival date, sex, and length of each spawner drawn randomly from distributions defined by model parameters.

The baseline conditions used as a basis for simulation experiments include survival and food availability parameters calibrated as described by Rallsback et al. (2013), except that the risk of predation by larger fish was reduced (parameter `mortFishAqPredMin` changed from 0.94 to 0.98) to produce a closer balance between fitness offered by anadromy and residence. Values for all inSALMO-FA parameters are in the online Supplementary Material¹.

Simulation experiments

We conducted a series of experiments to analyze inSALMO-FA and what it tells us about how individual decisions interact with environment, competition, and other complexities to determine the numbers of anadromous and resident fish. First, like Satterthwaite et al. (2009, 2010) we analyzed the anadromy behavior itself to understand the conditions under which model individuals select anadromy or residence.

We then looked at how population-level results — the number of *O. mykiss* juveniles becoming smolts or residents — vary with overall growth and survival conditions. Differences between these results and those of the behavioral theory indicate complexities and feedbacks due to population-level processes. We varied growth conditions by simulating five values of the two reach-level parameters for food availability (drift concentration and production of benthic food), ranging from 33% to 300% of their baseline values. For survival conditions, we used five values of the parameters controlling daily survival probability of predation risk, from 98% to 102% of baseline values (corresponding to a $\pm 50\%$ range in the probability of surviving for 30 days). Our experience calibrating inSALMO indicated that these ranges were broad enough to strongly affect individual growth and survival throughout the population.

The final set of experiments was a sensitivity analysis of the anadromy theory parameters. Like Satterthwaite et al. (2009, 2010), we used sensitivity analysis to identify processes especially important for producing smolts or in need of additional study. We examined the effects of the parameter values on both the theory and on population-level results by varying one parameter at a time over a wide range around the standard value (Table 2).

Results

Anadromy behavior

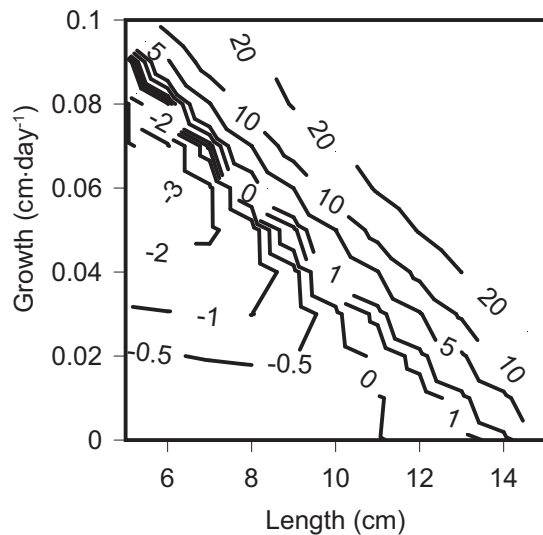
To better understand our theory for how a juvenile's decision of whether to smolt depends on its size, growth rate, survival probability, sex, and the date, we plotted the “anadromy benefit” — the difference between F_A and F_R ; fish select anadromy when its value is positive — over broad ranges of conditions. First we examined how the anadromy decision depends on length and growth at midsummer (Fig. 1). The theory predicts that at a typical survival probability, smaller fish should remain resident except at high growth rates, while fish that have already attained ~ 12 cm should be anadromous for any positive growth rate. At low growth rates and lengths less than ~ 12 cm, there is little difference between anadromy and residence (anadromy benefit is near zero) because neither option offers high expected fitness.

The effects of survival and growth on the anadromy decision differed relatively little between early and late summer (Fig. 2). The decision is driven mainly by survival; the boundary between positive and negative anadromy benefit varies little with growth. Especially early in summer there is little difference in expected fitness between anadromy and residence (between F_A and F_R) when neither survival nor growth are high, because expected probability of survival to, and size at, reproduction are low for both options.

Population level

To understand results at the population level, it is first important to understand the general fate of juveniles. In the baseline simulation, 218 600 juveniles emerged from the redds. Of those,

Fig. 1. Contour of anadromy benefit versus length and growth rate for an age 0 female on 1 July, with daily survival probability of 0.98.



30% outmigrated as juveniles shortly after emergence, without rearing successfully. Another 47% of juveniles died before choosing between anadromy and residency. Of the juveniles that survived to select a life history, 41 500 became presmolts and only 170 became resident prespawners. Of the presmolts, only 4150 (10%) survived to actually migrate out as smolts. The vast majority of presmolts selected anadromy as soon as the 30-day delay in decision-making after emergence ended.

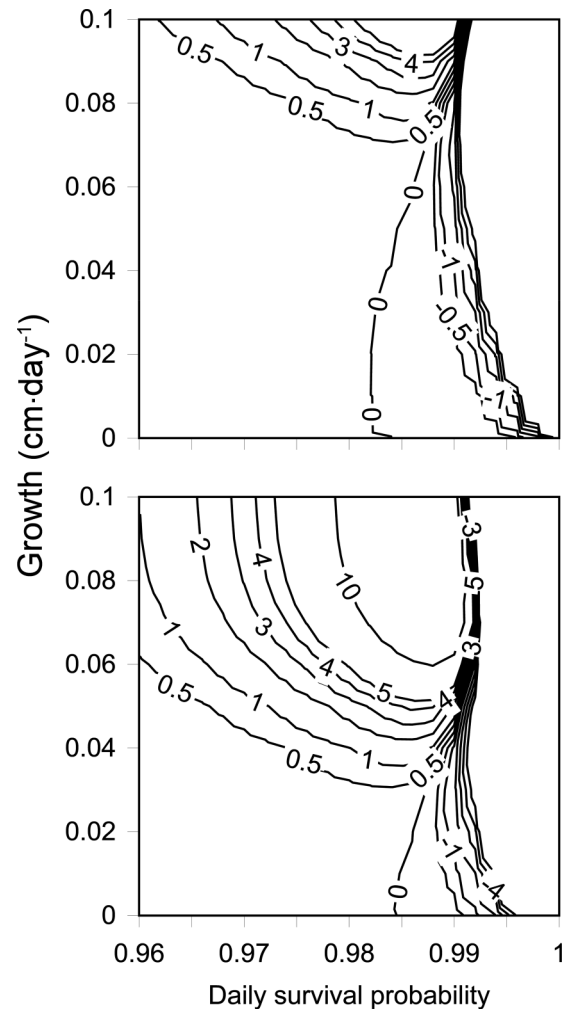
When we varied survival and growth conditions (Fig. 3), the number of juveniles selecting anadromy was highest at high food availability and medium survival, but there was no clear threshold in survival above which anadromy was not chosen. The peak number of smolts occurred at higher survival than did peak selection of anadromy (middle versus top panel of Fig. 3). The number of juveniles choosing resident spawning increased with survival, with little effect of food availability.

Parameter sensitivity

Figure 4 illustrates effects of variation in the anadromy parameters (Table 2) on the anadromy behavior and on population-level results. The parameter for the maturity decision interval (number of days before spawning season at which juveniles commit to residence) was not included in the behavioral theory analysis because it does not affect decisions. This parameter had little effect on simulated smolt production because (under the baseline scenario) a large majority of juveniles commit to anadromy at the beginning, not the end, of the decision period. The memory list length value affects results because it is the minimum number of days after emergence at which a juvenile can become a presmolt. This parameter had little effect on the behavioral theory (it was assumed to control the date at which the decision is made; for each day added to its value, we added a day to the decision date), but had strong effects on simulated number of smolts. Its effect on smolt production is a consequence of the high mortality of juveniles; when the list length is low, juveniles can commit to smolting earlier, so more of them smolt and migrate out of the simulated system before dying. The strong effect of the smolt delay has a similar cause; the smaller the value of this parameter, the sooner presmolts can migrate out and the fewer of them die first.

Expected ocean survival had a relatively strong effect on the anadromy decision (maximum ocean survival was the only parameter that produced negative anadromy benefit, when its value was zero). However, its effect on smolt production decreased

Fig. 2. Contours of anadromy benefit as a function of expected survival probability and growth; juveniles select anadromy where the benefit is positive. The top panel represents early decisions: date = 1 May, length = 5 cm. The bottom panel represents late decisions: length = 10 cm at 1 October. Both panels represent females; results for males are very similar.



at higher-than-baseline values. Once maximum ocean survival reached a threshold (around 70% of the baseline value), almost all juveniles chose anadromy, so further increases had little effect.

Discussion

The theoretical framework for understanding and modeling facultative anadromy as an adaptive behavior (e.g., as applied by Satterthwaite et al. (2009, 2010)) is powerful and flexible for predicting anadromy decisions of individuals. Even though we simplified the framework by considering only common life histories and eliminated the need for a rigid decision timetable, our model produced anadromy decisions similar to those produced by the model of Satterthwaite et al. (2009, 2010) for fish of the age and size we addressed (e.g., compare our Fig. 1 with fig. 3 of Satterthwaite et al. 2009). Both models predict more anadromy in age 0 juveniles with higher growth, larger size, lower freshwater survival probability, and higher expected ocean survival.

However, predicting how facultative anadromous populations are affected by management (e.g., how the number of smolts produced by a stream varies with flow, temperature, or habitat restoration) requires modeling not just the anadromy behavior but also how population-level responses emerge from individual varia-

Fig. 3. Results of population-level sensitivity to survival and growth conditions. The X axis represents the intensity of simulated predation due to both fish and terrestrial animals, as a percentage of survival under baseline parameter values; risk decreases from left to right. The Y axis represents simulated food availability, as a percentage of baseline conditions. Top panel: Number of juveniles selecting anadromy (number of presmolts). Middle panel: number of smolts that outmigrated. Bottom panel: Number of prespawners (juveniles that chose resident spawning).

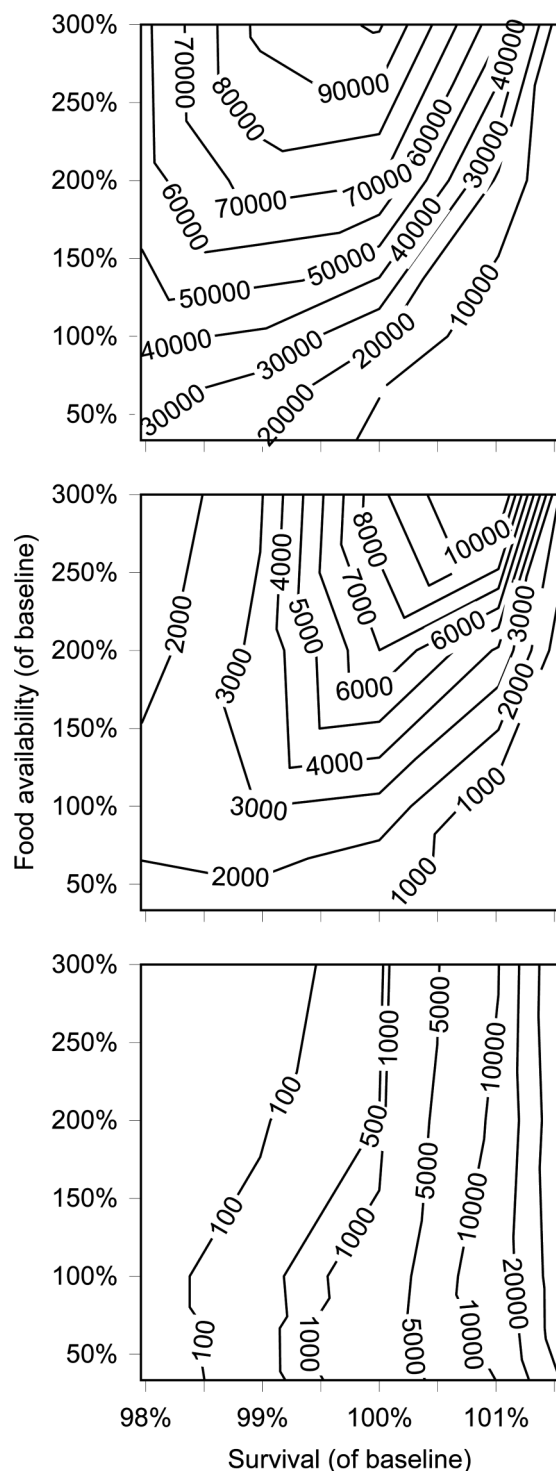
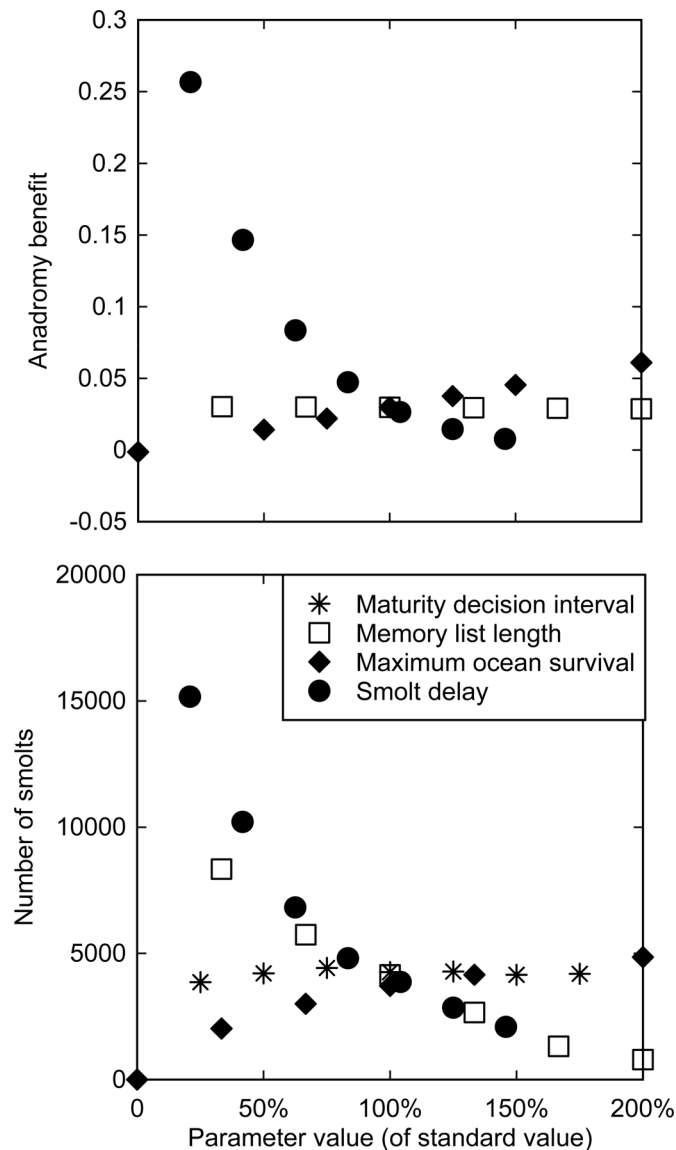


Fig. 4. Effects of anadromy parameters on anadromy benefit (top panel) in the anadromy theory; and number of outmigrating smolts (bottom panel) in simulation results.



tion, competition, environmental conditions, and adaptive behavior (Vincenzi et al. 2012). Understanding such emergent responses is exactly the realm of individual-based ecology and modeling (Grimm and Railsback 2005; Railsback and Harvey 2013). We developed inSALMO-FA and its predecessor models to understand and predict how stream salmonid population phenomena emerge from behavior and environmental conditions.

A primary objective of this study was to look for any ways that analyses based on behavioral theory alone (e.g., Satterthwaite et al. 2009, 2010; Benjamin et al. 2013) could be incomplete or misleading. Do such studies that model decisions of a typical individual, but not feedbacks of decisions within a population or population-level results such as smolt production, provide a useful basis for management decisions? In general the correspondence between approaches was encouraging; our model produced trends in smolt production that mostly correspond to its trends in the number of juveniles choosing anadromy. However, the model also produced several noteworthy differences between how the behavioral theory varied with growth and survival conditions (Fig. 2) and how the number of juveniles choosing anadromy and

the number of outmigrating smolts varied (Fig. 3). First, smolts were produced over the entire range of food availability and survival combinations, not just when food availability was high or survival low as would be expected from the behavioral theory. This difference arises no doubt from habitat heterogeneity and individual variability. Even when overall food availability is low, there can still be patches of habitat offering high growth and high survival; the lucky individuals that emerge first and find such patches can maintain high growth (through size-based competition) and are likely to become anadromous. And even when food availability is high, competition for food and habitat results in the best option for some individuals (most likely, those emerging latest and hence having low competitive ability) being to select habitat offering low growth but high survival; such individuals are likely to remain as residents. Second, we observed regions in the food availability–survival space where the number of both anadromous and resident fish were high (high food availability and moderately high survival) and regions where both anadromous and residents were few (low survival).

These two differences indicate that the behavior theory paradigm of seeing the growth–survival space (or size–growth space) as divided into regions whether fish are either anadromous or resident is inadequate at the population level. Instead, in our simulations the growth–survival space grades among regions that are good and bad for juvenile production in general and regions where the anadromous life history is more and less dominant. Our results indicate that production of smolts is highest at high (but not extremely high) survival and high food availability — conditions that also produce large numbers of residents. In our simulations anadromy dominates except when survival is high and food availability low. (When both food availability and survival are low, the model predicts little difference between the expected fitness of anadromy and residence, so its predictions in that region are likely to be especially uncertain. However, this uncertainty is unimportant because very few presmolts or residents survive to reproduce when growth and survival are both low.)

A third difference between behavioral theory and population-level results is that in our simulations lower survival did not generally produce more smolts. The anadromy theory did cause more juveniles to select anadromy as survival decreased, under most food availability conditions (top panel of Fig. 3). However, the number of these fish that survived to actually migrate downstream as smolts was nearly constant or decreased as survival decreased over most of the food–survival space (middle panel of Fig. 3). This difference is of course because lower survival causes more of the presmolts to die before they actually smolt.

The parameter sensitivity experiment provides a fourth difference between individual decisions and population responses. This experiment showed that the strongest effects of parameter values on simulated smolt production were not because the parameters strongly affected the relative reproductive output expected from anadromy versus residence, but because the parameters affected how likely anadromous juveniles were to survive until they left their natal stream. This sensitivity is a consequence of the behavioral theory assuming that survival in fresh water is a daily process, so the longer an individual stays in fresh water the lower its probability of surviving until outmigration, while survival from outmigration through adulthood is independent of the duration of those life stages. (Because it ignores variation among presmolts in how long they are in fresh water, the behavioral theory of Satterthwaite et al. 2010 does not have this sensitivity.) Sensitivity of smolt production to the time that elapses between emergence and downstream migration is in part an artifact of our modeling survival after outmigration (S_0) as independent of time. If smolts migrating downstream earlier then spend more time in downstream waters where survival is comparable to (or lower than) that in the natal stream, then our theory could overestimate the fit-

ness benefits of early outmigration. On the other hand, if early outmigration means earlier achievement of adult size and a resulting decrease in predation risk, then reducing the time of exposure to freshwater risk could have a survival benefit that partially offsets the additional risk of smaller size at outmigration. We should perhaps think of outmigration timing as driven not just by size but as a trade-off between the benefits of size to smolt survival against the time that presmolts and smolts are exposed to the different levels of predation risk in the habitats they migrate through.

Our results therefore indicate two considerations for using behavior-theory-only analyses to support management decisions. First, instead of just identifying regions (in growth–survival space or size–growth space) where individuals should be anadromous or resident, it is useful to look at how strong the advantage of anadromy or residence is (as did Satterthwaite et al. 2010). Our simulations did not produce distinct switches between anadromy and residence but, because of habitat heterogeneity and individual variation, gradients in the frequency of the alternative life histories. The second consideration is recognizing that while low stream survival may favor anadromy, it is likely to produce few smolts. The exceptions to the general conclusion that simulated smolt production followed the behavioral theory were in results for low survival scenarios; in our lowest survival scenarios there was not a strong, positive relation between the number of juveniles selecting anadromy and the number of smolts produced. Low survival in natal streams may encourage more juveniles to select anadromy while not actually producing more smolts because fewer presmolts survive to migrate downstream. Management to increase growth (e.g., by providing moderate velocities and velocity shelter; Railsback et al. 2013) seems a safer approach for promoting anadromy, even if it also produces more residents.

Here we did not explore the capability of inSALMO-FA to simulate the effects of habitat characteristics (e.g., flow, temperature, and turbidity regimes; channel shape) on individual growth, survival, and anadromy behavior and the resulting production of anadromous and resident fish. We also simply assumed that variation among individuals in size and growth (within each model run) emerged from factors such as date and size at emergence and the ability of individuals to find good rearing habitat. However, this model is well-suited for exploring alternative hypotheses for facultative anadromy. For example, it could be used to test whether innate differences among fry (e.g., in size and growth, metabolic rate; Chernoff and Curry 2007; Hayes et al. 2012; Sloat and Reeves 2014) are sufficient to explain anadromy rates within the theoretical framework we use, or whether they suggest another mechanism driving facultative anadromy.

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