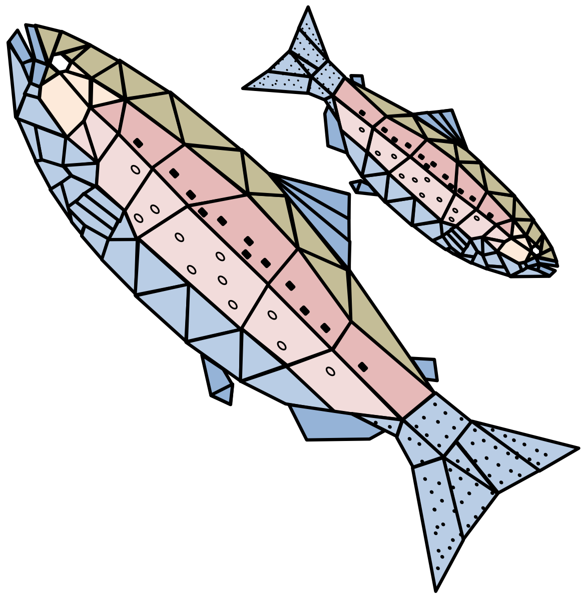
inSALMO-FA: A Version of *inSALMO* for Facultative Anadromous Trout Model Description and Initial Analyses



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1 Introduction

This document reports products of Task 7 of the inSALMO project conducted by Lang Railsback & Assoc. and Redwood Sciences Laboratory for the US Fish and Wildlife Service. Task 7 is to modify the inSALMO individual-based salmon model to include steelhead (*Oncorhynchus mykiss*). Although this task and document are focused on steelhead, the model is potentially applicable to other facultative anadromous salmonids such as Atlantic salmon and brown/sea trout. Hence, this version of the model is called inSALMO-FA for 'facultative anadromous'.

2 Model Description

This section describes the modifications and additions made to inSALMO to represent facultative anadromous salmon, especially steelhead. It supplements the complete description of inSALMO as formulated for obligate anadromous salmon species (Railsback et al. unpublished). inSALMO-FA can represent both obligate salmon, exactly as in inSALMO, as well as facultative anadromous trout as described in this document.

The description follows the ODD (Overview, Design Concepts, and Details) model description protocol (Grimm et al. 2010) except for not duplicating information in the previous description of inSALMO. We use the term FAT (for facultative anadromous trout) for the simulated fish. As our example FAT, we use the term *O. mykiss* to refer to rainbow trout and steelhead (both resident and anadromous life histories of *O. mykiss*).

2.1 Overview

2.1.1 Model purpose

The purpose of inSALMO-FA is to understand and predict how river management affects life history expressions of *O. mykiss* and other facultative anadromous species. The river management variables are the same addressed by previous versions of inSALMO and inSTREAM: flow, temperature, and turbidity regimes; channel shape, hydraulics, and cover availability; and biological factors such as food production, predation, and species composition.

The specific life history issue addressed by inSALMO-FA is how many juveniles become anadromous vs. remain resident. *O. mykiss* have a very flexible life history. Spawning is typically in spring or early summer, with fry emerging in early-mid summer. Resident *O. mykiss* of all ages can potentially smolt and migrate to the ocean; data from Clear Creek (USFWS 2010; 2011) indicate that smolt-size *O. mykiss* emigrate throughout the year. Those remaining resident may, each spring, mature and spawn or remain immature. *O. mykiss* that have migrated to the ocean may, each fall or winter, either remain in the ocean or mature and migrate back to freshwater for spawning. *O. mykiss* do not necessarily die after spawning, so this cycle of life history decisions can be repeated after spawning.

Anadromous *O. mykiss* of California's Central Valley are listed as endangered under the federal Endangered Species Act, so management emphasis is on promoting anadromy. However, management actions made to benefit other listed salmonid species, e.g., improving rearing habitat for Chinook salmon, potentially could encourage *O. mykiss* juveniles to remain resident.

Further, the complex life history of steelhead means that it is difficult to predict whether specific management actions promote vs. discourage anadromy (Satterthwaite et al. 2010).

Specific kinds of questions that inSALMO-FA is intended to address include: (1) Would improved rearing conditions (e.g., additional feeding and hiding cover) produce more or fewer anadromous individuals? (2) Would management actions that reduce growth and survival in late summer encourage anadromy, enough to offset any increased mortality?

Because the model's purpose does not include understanding or predicting the complete details of steelhead life history, it makes several very important simplifications. The model limits life history options to several that appear to dominate in Central Valley rivers (Sogard et al. 2012): smolting during the first two years of life (age 0, age 1, ending at the end of the calendar year after the year of birth), and resident maturation at age 1 in preparation for spawning at age 2. inSALMO-FA also does not attempt to reproduce complex male life history strategies such as "sneaker males" that mature and attempt spawning at small size. Nor does the model represent spawning by residents; juveniles that decide to spawn without ocean migration simply remain in the model without spawning until they die or the simulation ends. (The model could be modified to represent spawning by resident FAT relatively easily, but doing so would make results more difficult to understand. Because residents often spawn earlier than anadromous steelhead, neglecting resident spawning results in a narrower range of juvenile emergence dates.) No resident trout are assumed present at the beginning of a simulation, so juveniles from the first simulated year do not have older residents to compete with.

2.1.2 Entities, state variables, and scales

inSALMO-FA includes only one type of entity not in inSALMO: a new fish species to represent facultative anadromous salmonids. These facultative anadromous trout (FAT) entities are treated as a separate subclass of fish, allowing selected traits to differ from those of salmon as modeled in inSALMO. (Both obligate and facultative anadromous types can occur in inSALMO-FA; obligate salmon behave as in inSALMO and continue to be represented by the software's "Trout" class.)

The FAT have a state variable, *lifestageSymbol*, representing its life history trajectory. In inSALMO, this variable had values of either "juvenile" or "adult". In inSALMO-FA, the value of *lifestageSymbol* is set to "juvenile" when a fish emerges from its redd, to "presmolt" if the fish decides to smolt, to "smolt" when a presmolt actually begins its outmigration, and to "prespawner" if the fish decides to prepare for spawning.

FAT also have two variables representing memory of the growth rates (*growthMemoryList*) and survival probabilities (*survivalMemoryList*) they have recently experienced. These variables are lists with length equal to the fish parameter *fishMemoryListLength* (number of days). Decisions based on memory of recent growth and survival therefore use memory of the past *fishMemoryListLength* days (Section 2.3.3.7). The current day is included in these memory lists at the time they are used for life history decisions.

2.1.3 Process overview and scheduling

Several changes are made to inSALMO's processes and scheduling. Each simulated fish still executes a habitat selection action each daily time step but the action differs among life history stages.

- The action is unchanged for adults.
- Individuals with *lifestageSymbol* = "juvenile" execute habitat selection as in inSALMO except that outmigration is allowed only for a limited time after the individual emerges from its redd (Section 2.3.3.1).
- Individuals with *lifestageSymbol* = "presmolt" use a modified habitat selection action described in Section 2.3.3.2.
- Individuals with *lifestageSymbol* = "smolt" only move downstream, using methods described in Section 2.3.3.3.
- Individuals with *lifestageSymbol* = "prespawn" use a modified habitat selection action described in Section 2.3.3.4.

inSALMO-FA includes one new fish action, which is making life history decisions. The action executes three submodels: the presmolt decision made by juveniles (Section 2.3.3.5), smolting by presmolts (Section 2.3.3.6), and the maturity decision made by juveniles (Section 2.3.3.7). This action is executed at the end of the daily fish action schedule—after fish have selected habitat, grown, and experienced mortality. The action is executed in descending order of fish size, though execution order does not matter. This action is ignored by obligate anadromous salmon.

2.2 Design concepts

2.2.1 Basic principles

The basic principles incorporated in inSALMO-FA are a life history decision-making framework established for *O. mykiss* and other optionally anadromous salmonid species (especially, Atlantic salmon) from empirical and modeling work (Metcalfe et al. 1988, Metcalfe 1998, Grand 1999, Mangel and Satterthwaite 2008, Satterthwaite et al. 2009). This framework includes the assumptions that:

- Life history decisions are made to maximize expected future reproductive success, which depends on both survival to and size at spawning;
- Decisions are made in advance of when they are implemented (e.g., a juvenile decides to smolt in the spring and actually smolts and migrates out to the ocean the following fall);
- Decisions are based in part on whether individual fish have met thresholds in current size and growth rate; and
- Decisions affect behavior between the time they are made and implemented, e.g., by causing fish that have decided to smolt and outmigrate to grow more rapidly.

2.2.2 Emergence

The key output of inSALMO-FA, which is different from that of inSALMO, is the number of FAT that choose to migrate to the ocean. This output emerges from input representing the number and size of spawners, environmental conditions that affect survival and growth, and the adaptive trait used by FAT to make the anadromy decision.

2.2.3 Adaptation

The adaptive trait added to inSALMO-FA is whether a juvenile FAT should remain resident or smolt and migrate to the ocean. (Other adaptive life history traits of *O. mykiss*, including when to mature and when to return from the ocean, are not necessary for inSALMO-FA's purpose.)

This smolting trait differs from the outmigration trait for salmon in inSALMO. The outmigration trait for salmon represents voluntary or involuntary movement downstream, which is not necessarily a result of smolting and migration to the ocean. The outmigration trait is executed each simulated day, and leads to immediate outmigration. In contrast the smolting trait for FAT does not include the option of downstream migration without smolting; FAT can migrate downstream only if they have chosen smolting and migration to the ocean as a life history strategy. A further difference is that downstream migration occurs long after the smolting decision is made; a fish that decides to smolt remains in the stream until its future smolting time, and the decision to smolt affects its behavior during that time.

2.2.4 Objectives

Juveniles base their decision of whether to smolt or remain resident by comparing their expected fitness from the two alternatives. The expected fitness is evaluated as expected number of future offspring, considering both survival to reproduction and fecundity. The details (including the time horizon) differ between anadromy and residence (Section 2.3.3.5).

2.2.5 Prediction

The fitness measures used in the juvenile life history are based on explicit predictions of future size (length and weight) and survival probability. Future probability of surviving risk other than starvation is predicted by simply assuming it is equal to the mean survival probability over the previous memory period.

How future fish size is predicted is a very important assumption strongly affecting model results. We adopted the method of Satterthwaite et al. (2009) of assuming a fish's rate of growth in length (cm/d) remains constant over the time horizon, at the rate experienced during the memory period. This choice was based on evaluation of alternative assumptions: assuming constant growth in length produced reasonable predicted lengths at spawning for the residency fitness measure. The alternative of assuming constant growth in weight (g/d) produced unrealistically low predicted sizes, and its assumption that fish do not catch more food as they grow does not seem reasonable. The alternative of assuming constant relative growth (g/g body weight/d) produced unrealistically large future sizes.

2.2.6 Sensing

One new type of sensing is added: the ability of model juveniles to determine their average growth rate (cm/d) and survival probability over a period of previous days (Section 2.3.3.8). These mean rates are sensed without uncertainty or error, and all days in the memory period are given equal weight in determining them.

2.2.7 Interaction

As in previous versions of inSALMO, individual juvenile salmon interact with each other primarily by competing for food and feeding habitat. In inSALMO-FA, this interaction affects the anadromy decision as well as habitat selection and outmigration timing.

2.2.8 Stochasticity

None of the processes added to inSALMO to represent FAT are stochastic.

2.2.9 Observation

Model observation methods are modified by breaking statistical summary output written to files out by the additional fish variable *lifestageSymbol*. This change allows observation of how many life fish are in each life stage, and how many outmigrants are smolts.

2.3 Details

2.3.1 Initialization

No changes are made to model initialization; FAT are initialized the same way that salmon are in inSALMO.

2.3.2 Input data

Input data are unchanged from inSALMO. Initialization input for FAT is identical to that for other salmon.

2.3.3 Submodels

2.3.3.1 Juvenile habitat selection and outmigration

In inSALMO, juveniles decide to migrate downstream if their expected survival and growth in the current reach is less than an "expected success" function representing survival downstream, which increases with length. Outmigration typically happens very soon after emergence, for juveniles unable to find good rearing habitat, and then gradually as the individuals that do find good rearing habitat grow toward smolting size.

For inSALMO-FA, the smolting decision is modeled separately. However, because FAT can also move downstream in large numbers very soon after emergence (e.g., *O. mykiss* as indicated by the screw trap data from Clear Creek) inSALMO-FA still needs a process by which unsuccessful early juveniles can be moved downstream. Hence, for FAT we retain the juvenile outmigration process of inSALMO for the first few days after emergence: the number of days is equal to the parameter *fishMemoryListLength*. (Juveniles can outmigrate while their age in days is less than *fishMemoryListLength*.) Hence, this period of potential outmigration is also the period needed for new juveniles to develop a memory of recent conditions used in the smolting decision (Section 2.3.3.7). After a juvenile FAT has existed for *fishMemoryListLength* days, the smolting decision becomes the only process by which it can decide to move downstream. (However, at any time fish can still select habitat in adjacent reaches, upstream or downstream, as part of their habitat selection action.)

2.3.3.2 Habitat selection by presmolts

Presmolt individuals have already decided to migrate to the ocean. Because survival during migration and in the ocean is strongly dependent on length, presmolts have a strong incentive to grow rapidly, and growth acceleration in presmolts has been observed (Metcalfe et al. 1988). Hence, inSALMO-FA assumes that presmolts use a different objective in selecting habitat cells. Instead of selecting the cell that maximizes "expected maturity" as in inSALMO, presmolts select the cell that maximizes the fitness measure for anadromy defined in Section 2.3.3.5. This measure is the product of expected survival to smolting, expected ocean survival, and reproductive output for anadromous adults. The habitat selection method includes the following differences from how the fitness measure is evaluated in Section 2.3.3.5. Current average non-starvation survival rate S_C is replaced by the non-starvation survival probability at the habitat cell being considered. Current average growth rate G_C is replaced by the growth rate at the habitat cell being considered. The number of days until smolting T_S is the actual number of days between the current day and the date of smolting (but is always at least 1, so that growth and survival matter even on the day of smolting when T_S would be zero).

Presmolts do not use "outmigration" to move downstream into the next reach (or out of the model) if survival and growth is low. However, they can, like juvenile life stages of inSALMO, consider cells in adjacent reaches in their habitat selection decision.

2.3.3.3 Habitat selection (outmigration) by smolts

Once a FAT's value of *lifestageSymbol* is set to "smolt", it actively moves downstream. The methods for doing so are almost identical for those used in version 1.5 of inSALMO for downstream movement of outmigrants. Smolts move downstream by one reach per day and then select good habitat in the new reach; or are recorded as "outmigrants" when they exist the downstream-most reach. The steps are:

- Identifying any other reaches that are immediately downstream (its reach's list of other reaches which have their upper end connected to its downstream end; it is possible for there to be more than one such reach, e.g., if the channel splits around an island with separate reaches on each site).
- If there are no such downstream reaches, "migrating out" of the model as other outmigrants do.
- Creating a list of all cells in the immediately downstream reach(s) that currently meet two criteria: depth greater than zero and velocity less than the smolt's maximum sustainable swimming speed. This swimming speed calculated using the temperature of the smolt's starting reach, not of the downstream one it is migrating into.
- If the downstream reach(s) have no cells meeting the depth and velocity criteria, remaining in its current cell of its current reach instead of migrating downstream. (In this unexpected event, the code issues a warning statement.)
- If the downstream reach(s) do have cells meeting the depth and velocity criteria, moving to a randomly selected one of them, removing itself from its current cell.
- Executing the habitat selection action of presmolts, using 1 for the value of T_S. This allows the smolt to find a more profitable cell in its new reach.

2.3.3.4 Habitat selection by prespawners

Prespawners are FAT that have decided to spawn as residents. Hence, their objective in habitat selection is assumed to be to maximize their expected number of offspring at the next spawning season. Expected offspring is the product of expected survival to age-2 spawning and the expected number of offspring at age-2 spawning, as defined at **Residency fitness measure**, Section 2.3.3.5, with these changes. Current non-starvation survival rate S_C is replaced by the non-starvation survival probability at the habitat cell being considered. The growth rate G_C is replaced by the growth rate that the fish would obtain in the cell it is considering.

In the case of prespawners that survive past the start of the age-2 spawning period (the current day of the year is greater than the parameter *fishSpawnStartDay*), the time horizon used in the habitat selection fitness measure is the time until the next year's *fishSpawnStartDay*.

2.3.3.5 Life history update for juveniles

This action is executed by FAT with *lifestageSymbol* = "juveniles" to determine if their life history stage changes to "presmolt".

The first step in this action is to update the survival and length memories used in subsequent steps of the action. All FAT with *lifestageSymbol* = "juveniles" execute the memory update submodel (Section 2.3.3.7).

The FAT are assumed to become pre-smolts if their expected fitness from anadromy exceeds expected fitness from residence. This decision is repeated every day by each juvenile that meets three criteria:

- The number of days since emergence is equal to or greater than the parameter *fishMemoryListLength*,
- Age is less than 2 (age 2 and older residents are assumed to never smolt; this limit is hardwired in the code, not a parameter), and
- Value of *lifestageSymbol* is "juvenile" (the decision to smolt or mature, once made, is irreversible).

The life history decisions use predictions of future fish length and weight at the end of several time horizons. Even though these predictions are based on constant growth in length, the fitness measures take as inputs a rate of growth in weight (which allows consideration of starvation survival, which is based on both length and weight at the beginning and end of a time horizon). For life history updates, the growth rate input to the fitness measures is predicted by assuming the fish's condition is 1.0 (weight is "normal" for the fish's length) if the length growth rate is positive. Length at the end of the time horizon is calculated as current length plus the time horizon length (d) times the length growth rate (cm/d). (Growth in length can be zero but not negative.) If length growth rate is zero, then weight growth rate (G_C, g/d) is assumed zero. Otherwise, fish weight at the end of the time horizon is calculated from its predicted length assuming a condition of 1.0; and G_C calculated as the difference between predicted and current weight divided by the time horizon length.

Andromy fitness measure. The fitness measure for anadromy (F_A) is approximated as the expected reproductive output at the next return from the ocean; subsequent spawning is neglected. F_A is the product of expected survival to smolting (S_S), expected ocean survival (S_O), and the expected number of offspring of ocean migrants (O_O). These three terms are explained below.

Expected survival to smolting (S_S) is approximated as the *nonstarvSurvival* × *starvSurvival* terms of the *expectedSmoltSuccess* fitness measure used in inSALMO (Sect. 4.2.3.1 of Railsback et al. unpublished), with the following modifications. (The *starvSurvival* term is included to allow fish to make good decisions even if no options offer positive growth. Without this term all options that do not provide positive growth produce the same value of the fitness measure; with it, options with higher growth produce higher values of S_S even if growth is negative.)

First, the time horizon is T_S, the number of days until smolting. The value of T_S is a parameter *fishSmoltDelay* set to represent the time (d) taken for the smoltification process once a fish decides to smolt. However, the parameter value should reflect the time between when a smolt leaves the reaches modeled in inSALMO-FA and when it actually reaches salt water. If the distance is short (e.g., in coastal streams) then *fishSmoltDelay* should reflect the time needed for the smolt transformation. If the distance is long (as in the Sacramento River basin) then the value can be small because the transformation can take place as the fish migrates downstream.

Second, *nonstarvSurvival* is calculated as S_C^T_S, where the current non-starvation survival rate S_C is estimated as the mean daily survival probability experienced by the fish, in its selected habitat cell, over the past number of days defined by the parameter *fishMemoryListLength*. (S_C is the mean of values on the fish's *survivalMemoryList*; Section 2.3.3.7.)

Third, *starvSurvival* is calculated using growth in mass estimated as G_C (g/d), the mean daily growth experienced by the fish over the past number of days defined by the parameter *fishMemoryListLength* (Section 2.3.3.7).

Expected ocean survival S_O is a logistic function of fish length, as used by Satterthwaite et al. (2009):

$$S_O = \mathit{fishOceanSurvMax} \times \mathrm{logistic}(L_S).$$

The parameter *fishOceanSurvMax* is the maximum ocean survival. The length L_S (cm) is extrapolated from the fish's current length, weight, and growth rate during calculation of *starvSurvival*. The logistic function of L_S is defined by two parameters: *fishOceanSurvL1* and *fishOceanSurvL9* are the lengths (cm) at which survival is 0.1 and 0.9 of maximum. We re-evaluated these parameters, in part using recent data on smolt survival of Central Valley steelhead, and treating *fishOceanSurvMax* as a typical survival for a large but realistic-sized smolt (~20 cm length; Figure 1).

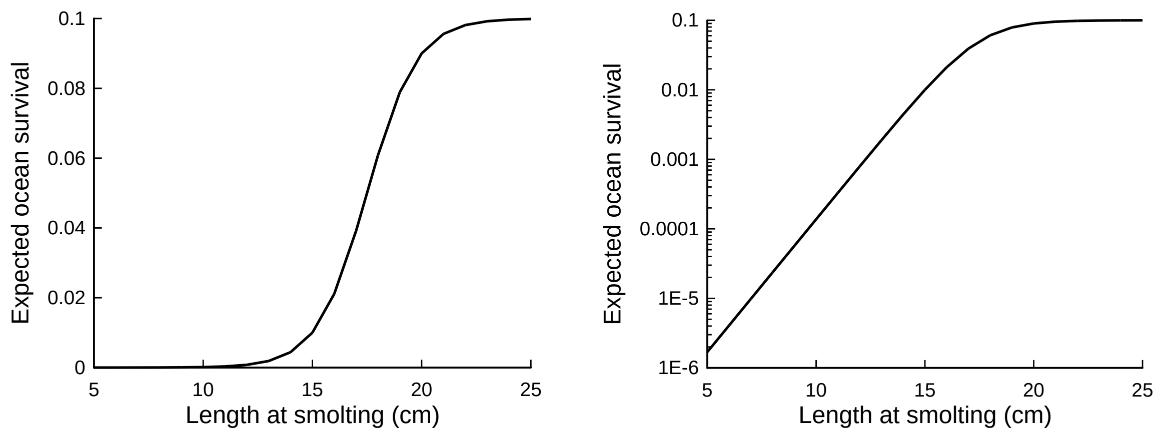

Figure 1. Ocean survival function. Right: Logarithmic y-axis scale. For each cm in fish length between 5 and 15, expected ocean survival increases by a multiple of 2.4.

The value of O_O differs between male and female FAT. Its value for females is the parameter *fishExpectedOffspringOceanFemale*. To reflect the lower reproductive benefit of size to males, we use a separate parameter *fishExpectedOffspringOceanMale* with a lower value.

Residency fitness measure. The fitness measure for remaining a resident (F_R) is approximated as expected reproductive output if the fish matures at age 2. (Maturation at age 1 is neglected as rare, and spawning at ages beyond 2 is neglected as a comparatively minor component of expected fitness.) F_R is approximated as the product of expected survival to age-2 spawning (S_2) and the expected number of offspring at age-2 spawning (O_2).

The value of S_2 is calculated the same way that expected survival to smolting (S_S) is for the anadromy fitness measure, except that the time horizon, instead of T_S, is T_2, the number of days remaining until the start of the spawning date window in the year when the fish is age 2. The spawning date window is defined by inSALMO parameter *fishSpawnStartDate*.[1]

The value of O_2 is calculated using inSALMO's equation and parameters for fecundity as a function of length:

$$O_2 = fishFecundParamA \times (L_2)^{\wedge} fishFecundParamB.$$

(For this calculation, the egg viability parameter is not considered; all eggs are considered potential offspring.) The length L_2 used in this calculation is the expected length at age-2 spawning, estimated in calculation of the starvation survival component of S_2. Males are assumed to receive the same value of O_2 as females.

Results of this submodel. Exploration of the submodel has illustrated several important characteristics. First, the main reason that anadromy becomes more beneficial as growth rate G_C increases is that the function for ocean survival increases with fish length more rapidly than does

[1] Therefore, if a fish's age is 0, then T2 is the number of days until *fishSpawnStartDate* plus 365; if its age is 1 and the current date is before *fishSpawnStartDate*, then T2 is the number of days until *fishSpawnStartDate* plus 365; if its age is1 and the current date is after *fishSpawnStartDate*, then T2 is the number of days until *fishSpawnStartDate*.

fecundity of resident fish. Second, the location of the dividing line between anadromy and residency (the zero contour on Figure 2-Figure 6) is strongly dependent on the fecundity parameters. In general, the submodel seems at least as sensitive to fecundity assumptions as to survival.

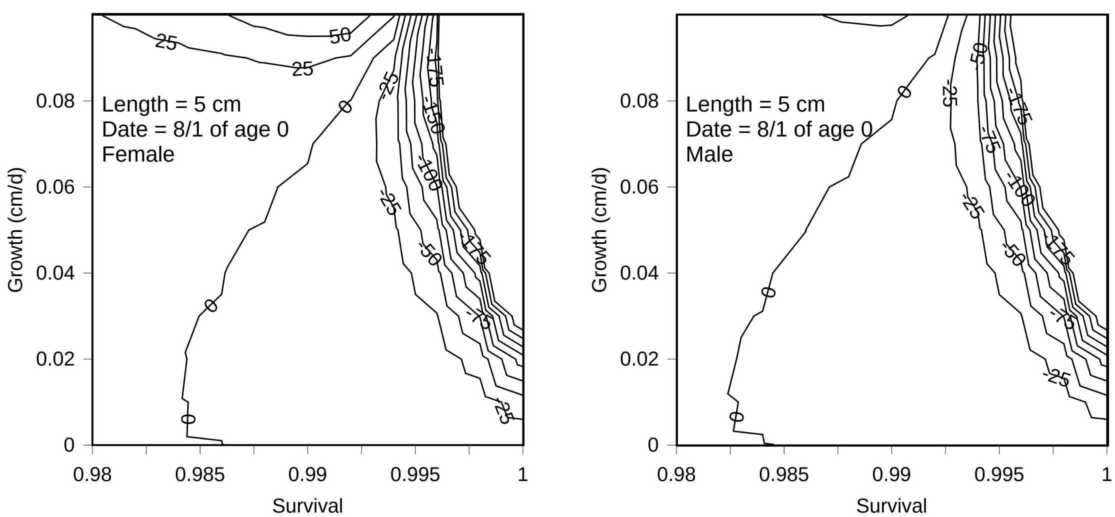

Figure 2. Anadromy benefit contours for 5-cm juveniles at their first August 1. The contoured value is the fitness measure for anadromy F_A minus the fitness measure for residency F_R.; hence, anadromy is chosen in the region with positive values (here, upper left). Juveniles remain residents unless their survival is low and growth relatively high.

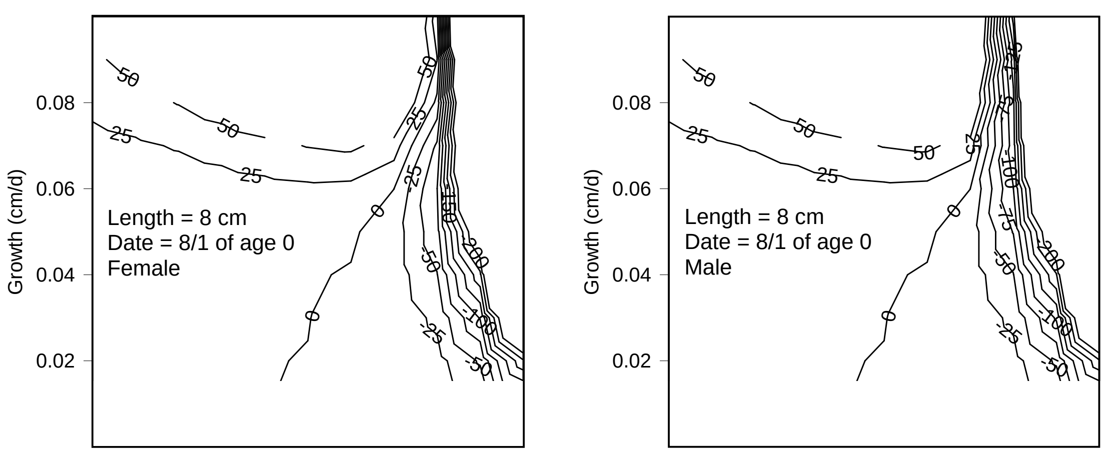

Figure 3. Anadromy benefit contours for 8-cm juveniles at their first August 1. Larger size, compared to Figure 2, increases the regions over which anadromy is chosen.

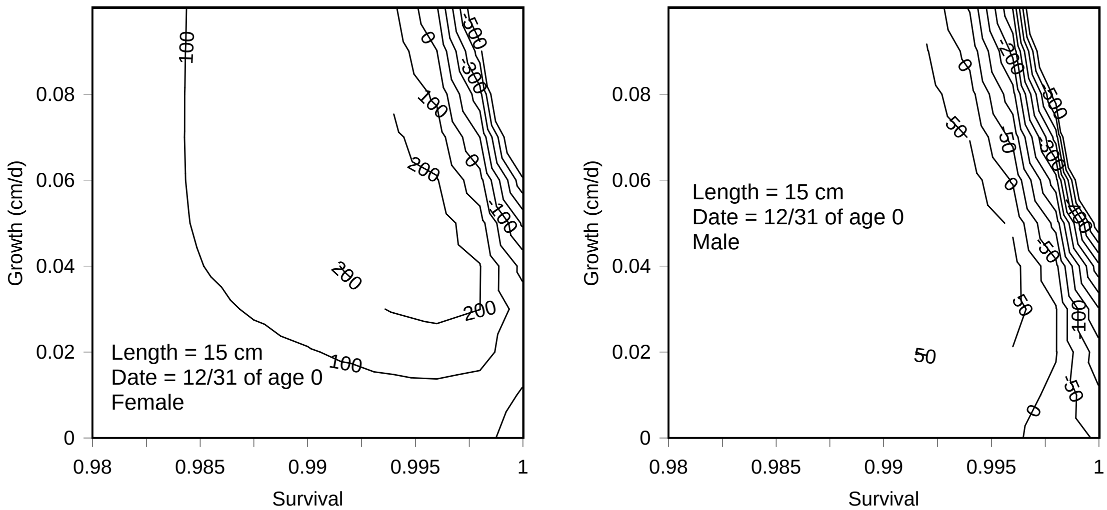

Figure 4. Anadromy benefit contours for 15-cm juveniles at the end of their first year. Residency is only chosen at high growth and survival.

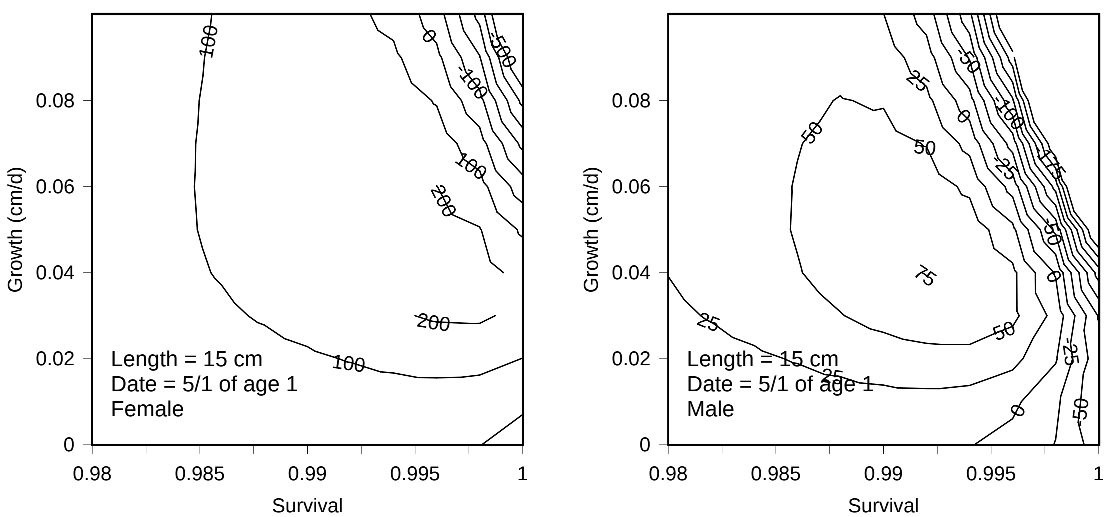

Figure 5. Anadromy benefit contours for juveniles at the May 1 of their second year, length = 15 cm. Clearer differences between males and females are apparent, with males choosing residency over a wide range.

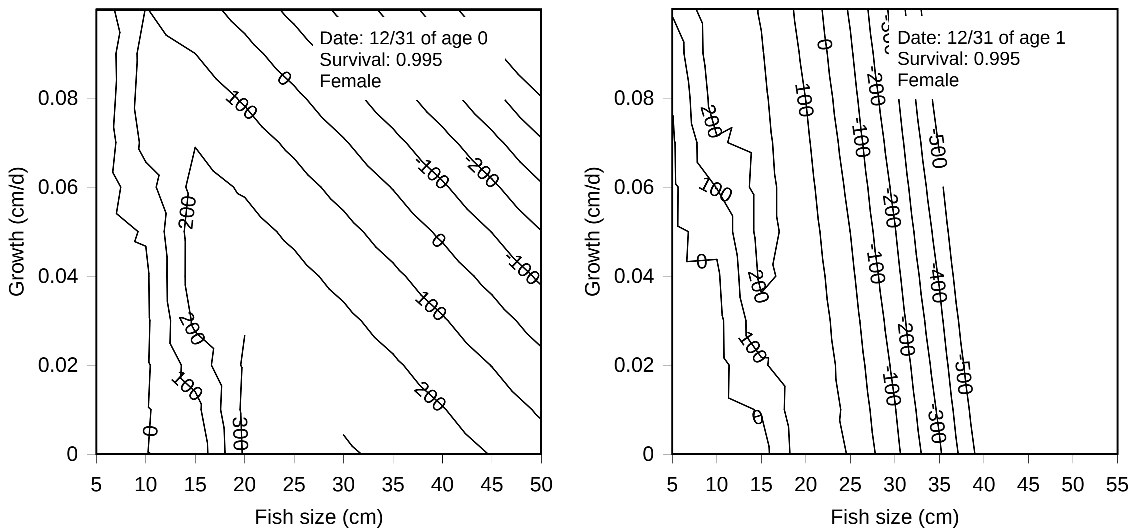

Figure 6. Growth-size contours for comparison to figures 5(A, C) and 7(A, C) of Satterthwaite et al. (2010).

2.3.3.6 Smolting

This transition turns presmolts into smolts. The decision is made very simply: presmolts turn into smolts when the number of days specified by parameter *fishSmoltDelay* has passed since the fish became a presmolt. A FAT's value of *lifestageSymbol* is set to "smolt" on the first day that the current date equals or exceeds *fishSmoltDelay* plus the date the fish had its value of *lifestageSymbol* set to "presmolt".

2.3.3.7 Maturity decision for resident trout

Because we assume residents mature only at age 2 (not age 1, and neglect delaying to later years) then the maturity decision is executed once, at a date appropriately before the age 2 spawning window. This date interval is set by the parameter *fishMaturityDecisionInterval* (days between the decision and the start of the next spawning period, as defined by the parameter *fishSpawnStartDate*. On the date when a juvenile is age 1 and the number of days until the next spawning period is equal to or less than *fishMaturityDecisionInterval*, the smolting decision is executed one last time. Fish that do not smolt at that time are assumed to stay and spawn; their value of *lifestageSymbol* is set to "prespawn".

2.3.3.8 Memory list updates

On each day of existence, each fish with *lifestageSymbol* = "juvenile" adds its current length and its non-starvation survival probability to the beginning of its memory lists *growthMemoryList* and *survivalMemoryList*. If the length of these lists is greater than the value of *fishMemoryListLength*, the last (oldest) value on each list is removed from it. Finally, the variables S_C and G_C used in the juvenile life history update action (Section 2.3.3.5) are updated. Mean growth rate G_C (cm/d) is updated by dividing the difference between first and last length on *growthMemoryList* by (*fishMemoryListLength* - 1). Mean survival rate S_C is calculated as the mean of all values on *survivalMemoryList*.

2.4 Parameters

All new parameters added to represent FAT are described and given values in Table 1. (All species must have all these parameters, even though they are not used by obligate anadromous salmon.) The complete set of parameters used for *O. Mykiss* are in Table 2. Many of the basic physiological parameters are those documented for rainbow trout by Railsback et al. (2009).

Table 1. Parameters related to *O. Mykiss* anadromy and their values.

Parameter	Meaning	Value for Clear Creek	Basis of value
fishMemoryListLength (integer)	Number of days used as recent memory of growth and survival in life history decisions.	30 d	Long enough to discount short-term events; short enough to capture seasonal changes.
fishSmoltDelay (integer)	Number of days between when a juvenile decides to smolt and when it transforms into a smolt and moves downstream.	120 d	The smolt decision typically takes place ~6 months before entering salt water. Much of the smolt transformation can take place during the long migration from Clear Creek to salt water. Satterthwaite et al. use values 120-140.
fishOceanSurvMax (float)	Maximum expected survival probability for outmigration, ocean, and return migration, in equation for expected ocean survival as a function of length.	0.10	Approximation based on smolt-to-adult return data from the Eel River, and data on survival of outmigrating steelhead smolts in the Sacramento basin.
fishOceanSurvL1 (float)	Length (cm) at which expected ocean survival is 0.1 of maximum.	15.0	Approximation based on smolt-to-adult return data in Alameda Creek.
fishOceanSurvL9 (float)	Length (cm) at which expected ocean survival is 0.9 of maximum.	20.0	Approximation based on smolt-to-adult return data in Alameda Creek.
fishExpectedOffspring OceanFemale (float)	Expected number of offspring (eggs) for anadromous females.	7100	Satterthwaite et al. (2009), who cited Shapovalov and Taft (1954). Satterthwaite et al. used this value as the lifetime egg production of an anadromous female; we use it to represent egg production at next spawning.
fishExpectedOffspring OceanMale (float)	Expected number of offspring (eggs fertilized) for anadromous males.	3500	Approximately half that of females, to reflect lower benefit of anadromous size to males.
fishMaturityDecision Interval (integer)	The number of days between when an age 1 juvenile decides to mature and the start of the next spawning period.	180	Approximated as 6 months before the start of resident spawning.

Table 2. Parameter values for *O. Mykiss*; the basis is provided for parameter values different from those used for Chinook salmon by Railsback et al. (unpublished).

Parameter	**Value**	**Basis**
fishCaptureParam1	1.6	
fishCaptureParam9	0.5	
fishCmaxParamA	0.628	
fishCmaxParamB	-0.3	
fishCmaxTempF1	0.05	
fishCmaxTempF2	0.05	
fishCmaxTempF3	0.5	
fishCmaxTempF4	1	
fishCmaxTempF5	0.8	
fishCmaxTempF6	0	
fishCmaxTempF7	0	
fishCmaxTempT1	0	
fishCmaxTempT2	2	
fishCmaxTempT3	10	
fishCmaxTempT4	22	
fishCmaxTempT5	23	
fishCmaxTempT6	25	
fishCmaxTempT7	100	
fishDetectDistParamA	4	
fishDetectDistParamB	2	
fishEnergyDensity	5900	
fishFecundParamA	0.11	Values for brown trout used by Railsback et al. (2009).
fishFecundParamB	2.54	
fishFitnessHorizon	90	
fishMaxSwimParamA	2.8	
fishMaxSwimParamB	21	
fishMaxSwimParamC	-0.0029	
fishMaxSwimParamD	0.084	
fishMaxSwimParamE	0.37	
fishMoveDistParamA	50	
fishMoveDistParamB	2	
fishOutmigrateSuccessL1	5	
fishOutmigrateSuccessL9	12	
fishRespParamA	30	
fishRespParamB	0.784	
fishRespParamC	0.0693	

Parameter	Value	Basis
fishRespParamD	0.03	
fishSearchArea	20000	
fishSpawnEggViability	0.8	
fishSpawnDefenseArea	200000	
fishSpawnStartDate	12/1	USFWS spawning survey data
fishSpawnEndDate	4/30	
fishSpawnDSuitD1	0.0	Gard (2011) spawning suitability criteria
fishSpawnDSuitD2	9.0	
fishSpawnDSuitD3	30.5	
fishSpawnDSuitD4	40.0	
fishSpawnDSuitD5	878.0	
fishSpawnDSuitS1	0.00	
fishSpawnDSuitS2	0.00	
fishSpawnDSuitS3	0.85	
fishSpawnDSuitS4	1.00	
fishSpawnDSuitS5	0.00	
fishSpawnMaxFlowChange	0.2	
fishSpawnMaxTemp	14	
fishSpawnMinTemp	5	
fishSpawnProb	0.2	
fishSpawnVSuitS1	0.00	Gard (2011) spawning suitability criteria
fishSpawnVSuitS2	0.00	
fishSpawnVSuitS3	0.87	
fishSpawnVSuitS4	1.00	
fishSpawnVSuitS5	0.66	
fishSpawnVSuitS6	0.00	
fishSpawnVSuitV1	0.0	
fishSpawnVSuitV2	18.0	
fishSpawnVSuitV3	40.0	
fishSpawnVSuitV4	46.0	
fishSpawnVSuitV5	94.0	
fishSpawnVSuitV6	119.0	
fishSpawnWtLossFraction	0.4	
fishTurbidExp	-0.0711	
fishTurbidMin	0.1	
fishTurbidThreshold	5	
fishWeightParamA	0.0134	Rainbow trout values from Railsback et al. (2009).
fishWeightParamB	2.96	
fishMemoryListLength	30	See Table 1.
fishSmoltDelay	120	

Parameter	Value	Basis
fishOceanSurvMax	0.1	
fishOceanSurvL1	15	
fishOceanSurvL9	20	
fishExpectedOffspringOceanFemale	7100	
fishExpectedOffspringOceanMale	3500	
fishMaturityDecisionInterval	180	
mortFishAqPredD1	20	
mortFishAqPredD9	10	
mortFishAqPredF1	18	
mortFishAqPredF9	0	
mortFishAqPredL1	4	
mortFishAqPredL9	18	
mortFishAqPredH1	200	
mortFishAqPredH9	0	
mortFishAqPredMin	0.94	
mortFishAqPredT1	15	
mortFishAqPredT9	8	
mortFishAqPredU1	5	
mortFishAqPredU9	80	
mortFishConditionK1	0.3	
mortFishConditionK9	0.6	
mortFishHiTT1	28	
mortFishHiTT9	24	
mortFishStrandD1	-0.3	
mortFishStrandD9	0.3	
mortFishTerrPredD1	5	
mortFishTerrPredD9	200	
mortFishTerrPredF1	18	
mortFishTerrPredF9	0	
mortFishTerrPredH1	500	
mortFishTerrPredH9	-100	
mortFishTerrPredL1	6	
mortFishTerrPredL9	3	
mortFishTerrPredMin	0.98	
mortFishTerrPredT1	10	
mortFishTerrPredT9	50	
mortFishTerrPredV1	20	
mortFishTerrPredV9	200	
mortFishVelocityV1	1.8	
mortFishVelocityV9	1.4	

Parameter	Value	Basis
mortReddDewaterSurv	0.9	
mortReddHiTT1	23	
mortReddHiTT9	17.5	
mortReddLoTT1	1.7	
mortReddLoTT9	4	
mortReddScourDepth	20	
reddDevelParamA	33000	Fit of the inSALMO development model to the inSTREAM model as parameterized by Railsback et al. (2009) for rainbow trout. These values reproduce the model of Railsback et al. (2009) except for slightly higher development rate at temperatures below 5C.
reddDevelParamB	-2.16	
reddDevelParamC	-8.22	
reddNewLengthMin	2.8	Estimate assuming steelhead eggs are somewhat larger than typical resident trout eggs.
reddNewLengthMax	3.2	
reddSize	20,000	USFWS observations in Clear Creek.

3 Input for Clear Creek *O. Mykiss*

3.1 Model reaches

Historically, most steelhead spawning in Clear Creek has been in the Upper Alluvial and Canyon reaches, upstream of Clear Creek Road. To represent this area, we developed USFWS hydraulic models and field habitat observations into inSALMO input for five sites: Dog Gulch and Spawn Area 4 (the uppermost two sites in the Upper Alluvial reach), and Kanaka and Above Igo in the Canyon reach. The upper two sites are generally shallow and high-velocity, while the lower two sites are narrower and made up of deep pools (Figure 7). (Input for the Peltier site was developed but not used in the analyses.)

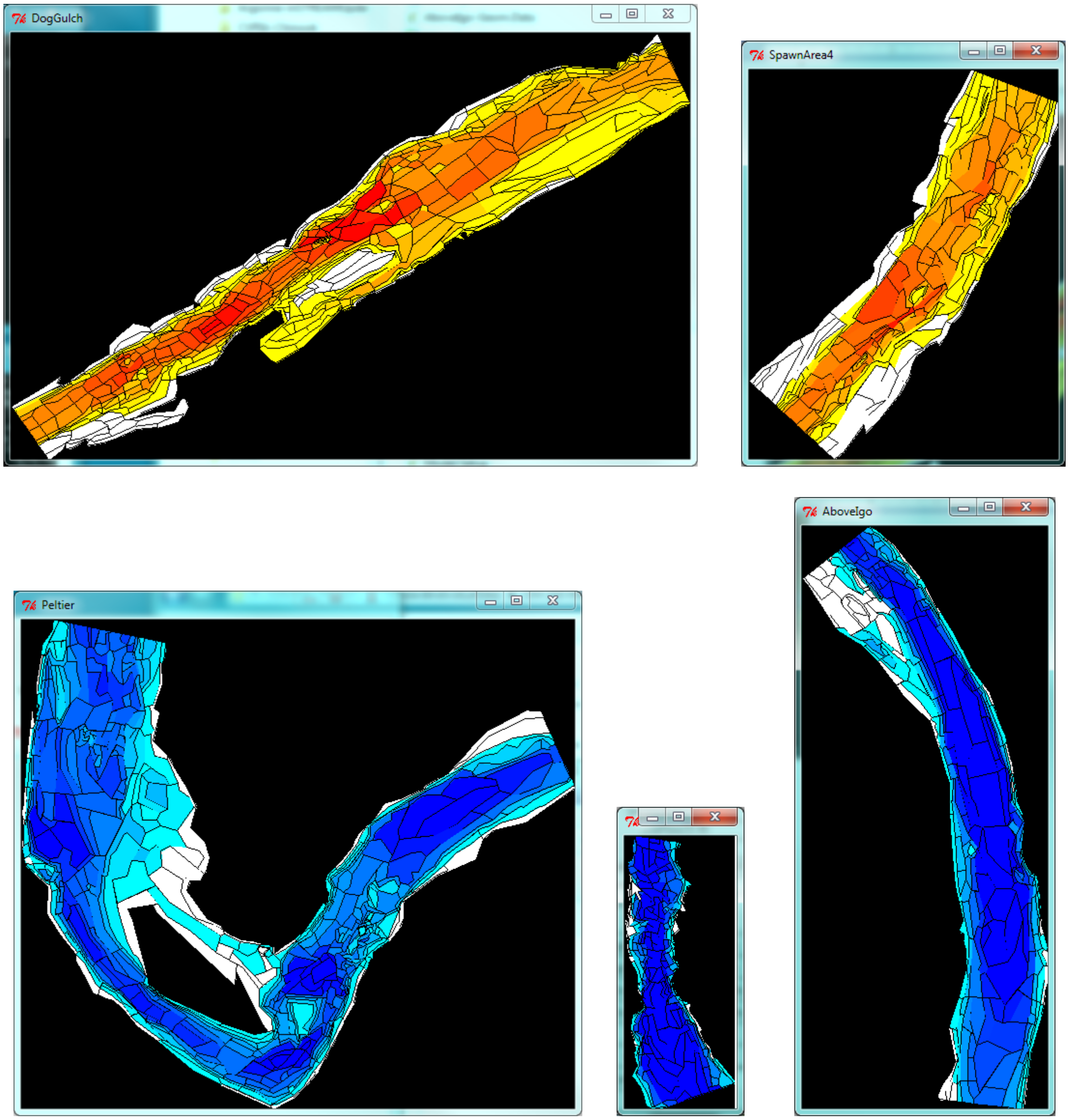

Figure 7. inSALMO habitat displays for (left to right, top then bottom) Dog Gulch, Spawn Area 4, Peltier, Kanaka, and Above Igo sites. Dog Gulch and Spawn Area 4 are shaded by velocity; the others by depth. All sites are at the same scale.

3.2 Spawner initialization

Steelhead spawner and redd data for Clear Creek are somewhat less abundant than Chinook salmon data, likely because steelhead are less abundant. USFWS redd surveys indicate counts of 27-124 (mean: 82) steelhead redds in all of the Upper Alluvial and Canyon reaches in annual surveys from 2003 through 2011. These redds were highly concentrated in the Upper Alluvial reach, with a large majority of redds within the first 3 km downstream of Whiskeytown Dam.

Very few measurements of steelhead spawner size are available for Clear Creek. Measurements of steelhead/rainbow trout spawners at Coleman Hatchery on Battle Creek in 2011 indicate length mean and standard deviation of about 40 and 5 cm. We used these values for the spawner length distribution.

Because the analyses reported here are intended to explore effects of river management on *O. Mykiss* anadromy and not to reproduce or explain historic observations, we used spawner initialization input that represents a somewhat larger and more stable spawner population than the Clear Creek data indicate. Considering the locations of the model reaches compared to where redd observations are highest, and the relative length of the model reaches, we used the following number of female spawners, for all simulated years: Dog Gulch—20, Spawn Area 4—15, Peltier—25, Kanaka—5, Above Igo—10.

The range of dates over which steelhead spawners appear to range from before December 1 (spawners were already present during the first December spawning surveys) through March. We therefore used an arrival date range of November 15 through March 31.

4 Model Analysis

4.1 Sensitivity to anadromy parameters

The first analysis of inSALMO-FA was to examine its sensitivity to the key variables affecting individual anadromy decisions: the memory length, expected ocean survival, the “smolt delay” (time between when an individual decides to smolt and when it actually begins smolt outmigration), and the “maturity interval” (time before spawning that an individual commits to resident spawning). We ran the model with the parameter values in Table 1 and Table 2, preliminary spawner initialization input, and four reaches: Dog Gulch, Spawn Area 4, Kanaka, and Above Igo. Habitat parameters were those obtained via calibration of Lower Alluvial reaches of Clear Creek to Chinook salmon data (Railsback et al. unpublished).

With the standard parameter values and input, no juveniles decided to remain resident. The simulation produced 470 outmigrant smolts with a mean length of 8.3 cm.

The first sensitivity experiment varied the value of *fishMemoryListLength*, which is (a) the number of past days used to calculate mean survival and growth rates for making the anadromy decision, and (b) the number of days after emergence before a juvenile FAT first makes the decision of whether to become a presmolt. The predicted number of smolts is highly sensitive to *fishMemoryListLength* (Figure 8); mean smolt size also varied with this parameter but not dramatically. As the list length was increased, the number of smolts dropped rapidly and became zero at around 100 d. More detailed analysis of results indicated that, while fewer smolts were produced at high values of *fishMemoryListLength*, no more prespawners were. The main mechanism by which this parameter affects the number of smolts seems to be in extending the period after emergence in which juveniles can outmigrate instead of having only the options of becoming presmolts or prespawners. Juvenile FAT can outmigrate only until their age in days equal *fishMemoryListLength* (Section 2.3.3.1). Higher values of *fishMemoryListLength* resulted in more juveniles outmigrating before deciding to smolt or spawn as residents, not more deciding to spawn instead of smolting.

A second important observation from this experiment was that survival of juveniles in the four simulated reaches was low. Low survival of non-smolts appears to be the main reason that few or no resident spawners were predicted in these experiments. Low survival likely results from the scarcity of shallow, low-velocity habitat in the four reaches we simulated (Section 3.1).

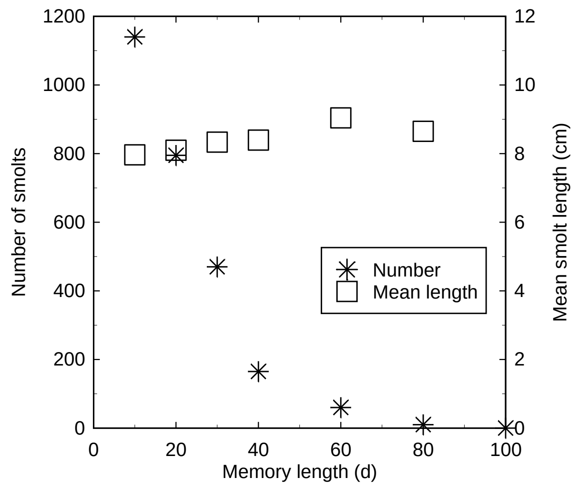

Figure 8. Sensitivity analysis results for *fishMemoryListLength*, which has a standard value of 30 days.

The maturity interval experiment varied parameter *fishMaturityDecisionInterval*. This parameter was found to have no effect on results, because all juveniles chose to smolt instead of maturing as residents.

The ocean survival experiment varied the maximum expected ocean survival (*fishOceanSurvMax*) around its standard value of 0.1. Parameter values near and above 0.1 produced results similar to the standard scenario, with 400-500 smolts with length 8-9 cm (Figure 7). However, as *fishOceanSurvMax* was decreased below about 0.05 the number of smolts decreased rapidly, presumably because more individuals chose to remain residents instead.

This experiment indicates that a value of *fishOceanSurvMax* below 0.05 will be appropriate for further experiments exploring how habitat affects the smolt decision because it results in juveniles choosing both anadromous and resident life histories. USED 0.02.

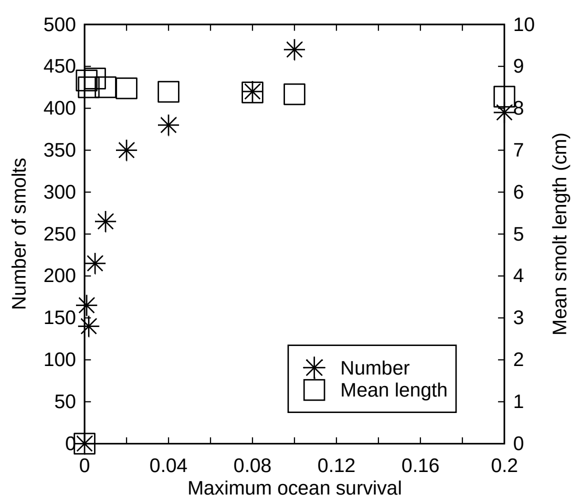

Figure 9. Sensitivity of simulated smolt production to expected ocean survival.

The smolt delay experiment varied *fishSmoltDelay* around its standard value of 120 d. This parameter strongly affected the number and size of smolts (Figure 8). However, this effect is not only because the parameter affects the life history decisions of juveniles but because it also affects survival of juveniles between when they decide to smolt (become presmolts) and when they actually migrate out. The shorter the smolt delay is, the less time the presmolts are present and exposed to mortality in the model. Smaller values of *fishSmoltDelay* therefore produce more smolts that outmigrate earlier and at smaller size.

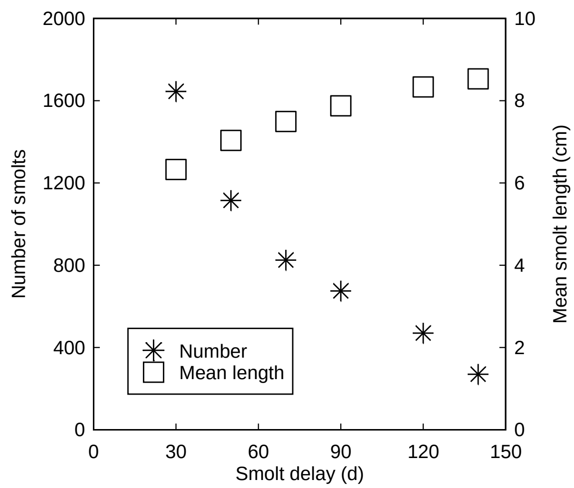

Figure 10. Sensitivity of simulated smolt production to the smolt delay.

4.2 Limiting factors analysis

This analysis used inSALMO's Limiting Factors Tool (LFT) to examine simulated sensitivity to management variables such as flow, temperature, and cover availability. We executed the LFT using the same four reaches as in the sensitivity analysis. The results we examined are the number and size of smolts. The parameter sensitivity analysis (Section 4.1) indicates several cautions for interpreting these results. The number of smolts produced is determined both by how many juvenile *O. Mykiss* emerge and survive their first few weeks, and by how many then decide to smolt. Some management actions that increase smolt production may do so by increasing the total number of juveniles while other actions may increase smolt production by increasing the fraction of juveniles that become anadromous instead of resident. The number of juveniles that commit to resident spawning is very low in all the LFT experiments, largely because survival until the date when they make this commitment (early June of the year in which they are age 1) is low in the reaches we simulated.

Most of the management and habitat variables examined in the LFT experiment had some effect on the number or size of smolts (Figure 11, Figure 12). Increases in base flow decreased smolt production, presumably by further reducing the availability of moderate habitat where growth and survival of newly emerged juveniles are high. (However, the very low smolt production at the highest flow scenario was because spawning was greatly reduced, apparently because the maximum spawning flow of 10 m^3/s was often exceeded during the mid-winter steelhead spawning season.)

Increasing food availability above the standard value (relative availability > 1) produced more and much larger smolts. However, increasing the availability of velocity shelter (which reduces the energy cost of drift feeding) produced no increase in smolt size and a relatively modest increase in the number of smolts.

Hiding cover availability had a strong effect on the number of smolts; doubling its availability approximately tripled the number of smolts. The level of piscivory risk had a consistent but relatively small effect. (In the simulations, predation by fish and by terrestrial animals caused approximately equal levels of mortality in presmolts, but piscivory caused much more mortality in juveniles before they became presmolts.)

Smolt production appears to have been highly density dependent in these simulations. Increasing the number of steelhead spawners by up to 10 times had relatively little effect on smolt numbers, and the availability of spawning gravel had no consistent effect.

Water temperature had strong effects on smolt production, with opposite effects between seasons. Summer temperature had a strong negative effect on smolt numbers, with a 4° decrease predicted to double smolt production. Winter temperature was positively related to smolt production, up to increases of 3°.

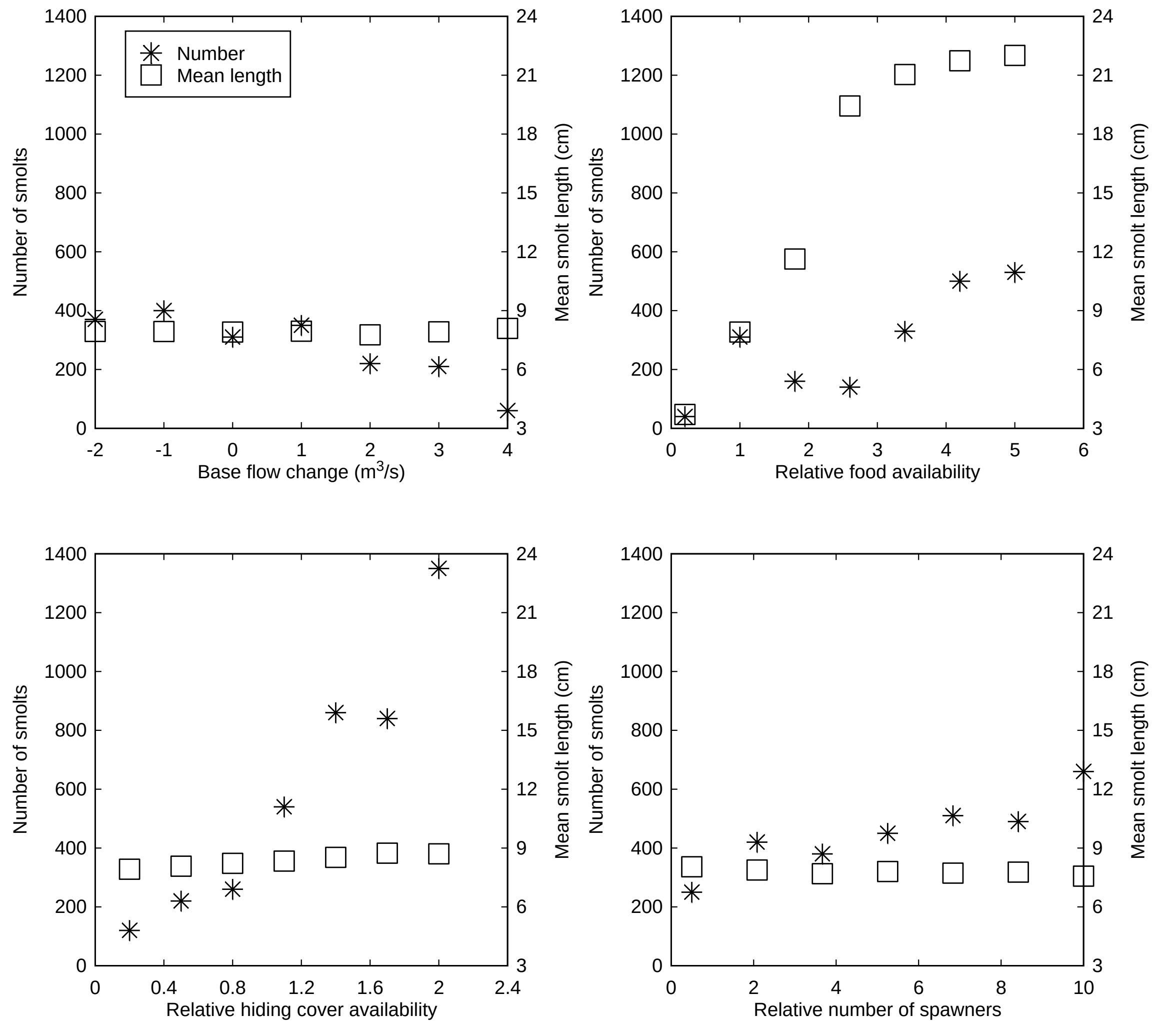

Figure 11. Limiting Factors Tool results for base flow, food availability, hiding cover, and number of spawners.

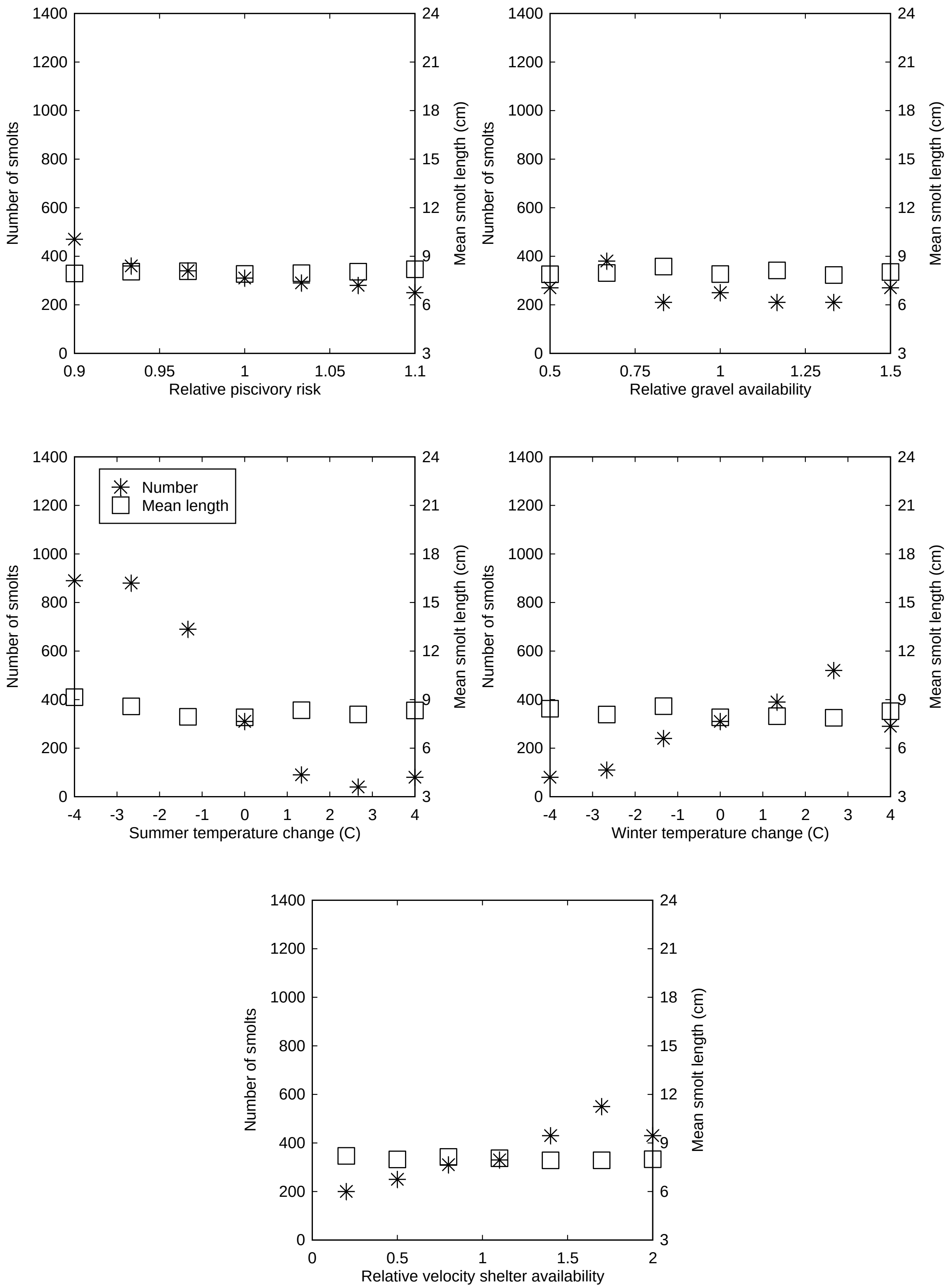

Figure 12. Limiting Factors Tool results for piscivory risk, spawning gravel availability, summer and winter temperature, and velocity shelter availability.

5 Software Information

The software for inSALMO-FA is distributed as a package that is separate but very similar to the standard inSALMO software, including its graphical user interface. This section describes the differences in software between inSALMO-FA and inSALMO.

5.1 Model code structure

In the Objective-C/Swarm code for inSALMO, behaviors of salmon are programmed in the class "Trout", and each species of salmon is a subclass of Trout that inherits all its behaviors from Trout. (Hence, the code includes a subclass of Trout named "FallChinook".) InSALMO-FA was implemented by creating a new subclass of Trout called "OMykiss"; this subclass inherits all its behaviors from Trout *except* those that are unique to facultative anadromous trout, as described in Section 2. Hence, the inSALMO-FA code can simulate both obligate anadromous salmon such as Chinook and facultative anadromous species such as steelhead at the same time (Figure 13). With very simple changes, additional species or races of both types could be added to the code.

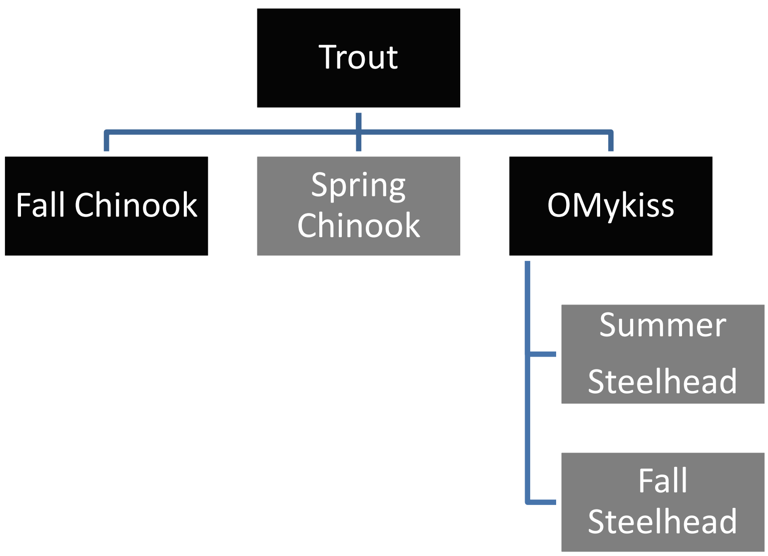

Figure 13. Class diagram for inSALMO-FA model code: each box represents an Objective-C class that models a salmonid species or race. Classes are subclasses of the class above them. Black boxes represent classes in the steelhead version of inSALMO-FA and grey boxes represent hypothetical subclasses that could be added to model additional fish species.

5.2 Software testing and test output

The inSALMO-FA software includes one new optional output file that reports the life history decision each juvenile makes each day (Section 2.3.3.5) and the information it uses to make the decision. This output file can be turned on by placing a line to the Model.Setup file with "`writeLifeHistoryDecisionReport        1`". The code will then write this output to a file named LifeHistory_Out.csv.

An Excel file documenting use of this optional output to test the life history decision code is included with the software products of this task. The file is named LifeHistory_Out-inSALMO-FA.xlsb.

5.3 Output changes

Outputs such as the number of life fish, number of fish dying of various causes, and number of outmigrants are labeled by species and life history stage (fish variable *lifestageSymbol*). In inSALMO, *lifestageSymbol* had values only of “adult” and “juvenile”. In inSALMO-FA, this variable has several additional values (Section 2.1.2). Hence, these outputs are automatically labeled by whether juveniles are presmolts, smolts, etc.

Some model outputs, and the Excel template files built into the inSALMO graphical user interface, separate results for outmigrants by whether the fish are “large” or not. With large outmigrants defined as having length > 5 cm, large outmigrants in inSALMO-FA can generally be assumed smolts. (Juveniles that migrate out before their age exceeds the value of parameter *fishMemoryListLength* rarely grow > 5 cm, at least with the parameters used in this report; and smolts are the only life stage allowed to migrate out after that time.)

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