Linking habitat, individual life history decisions, and population-level consequences in facultative anadromous salmonids

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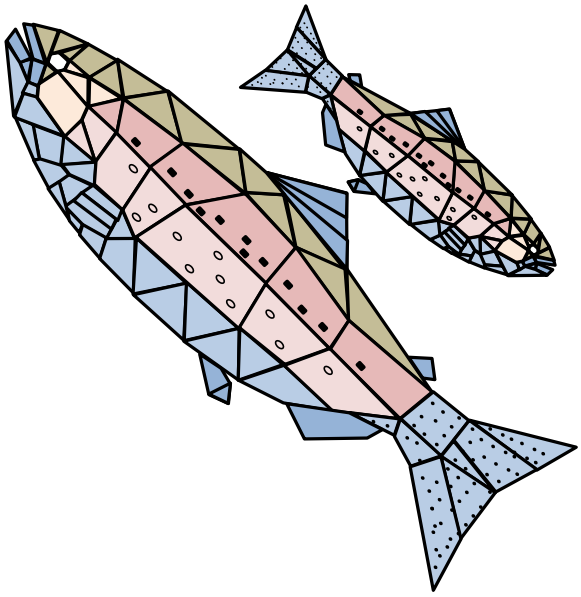
Supplementary Material

This document is a detailed description of the model inSALMO-FA, originally prepared as a help file packaged with the inSALMO-FA software. The document was produced in September 2013 by Lang Railsback & Associates for the US Fish and Wildlife Service.

Sections 1-3 describe how inSALMO-FA differs from its precedessor inSALMO, which is a model of strictly anadromous salmonids. The remaining sections describe inSALMO in detail.

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



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1 Introduction

This document describes inSALMO-FA, a model produced by Lang Railsback & Assoc. and Redwood Sciences Laboratory for the US Fish and Wildlife Service. The model is a modification of the inSALMO salmon model to include steelhead (*Oncorhynchus mykiss*). 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'.

This document is prepared as the help file to be packaged with the inSALMO-FA software. Section 2 is a description of how inSALMO-FA differs from version 1.5 of inSALMO. Section 2.5 describes how the software for inSALMO-FA differs from that of inSALMO. The complete description of inSALMO 1.5 is appended as sections 4 through 12.

2 Description of inSALMO-FA

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 unpublished).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 2.3.3.8). 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 2.3.3.8). 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 2.3.3.8).

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.

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 $S_C \text{^} T_S$, 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 2.3.3.8.)

Third, the calculation of *starvSurvival* uses length and weight predicted for the end of the time horizon as described above.

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

$$S_O = \textit{fishOceanSurvMax} \times \text{logistic}(L_S).$$

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).

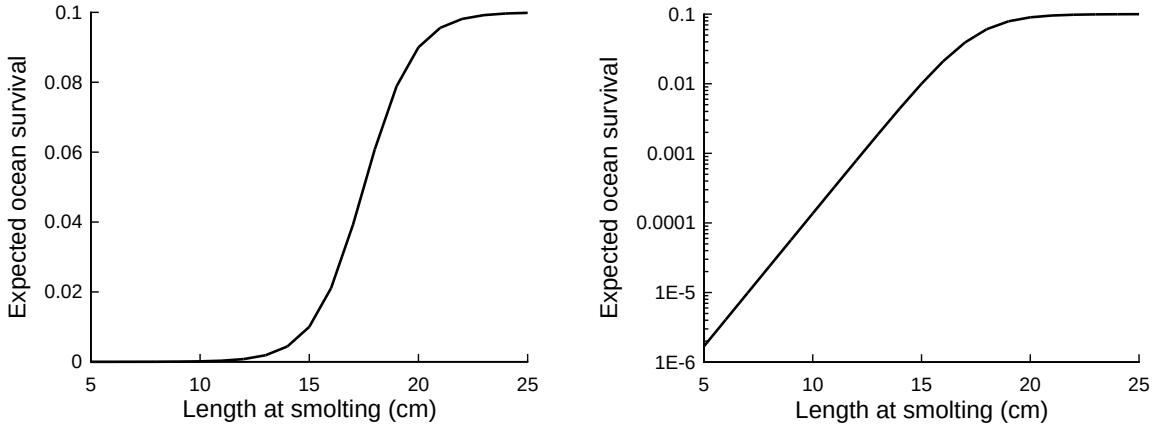

Figure 1. Ocean survival function. Right: Logarithmic y-axis scale. For each cm in fish length between 5 and 15, expected ocean survival increases by a multiple of 2.4.

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:

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

(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 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.

[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*.

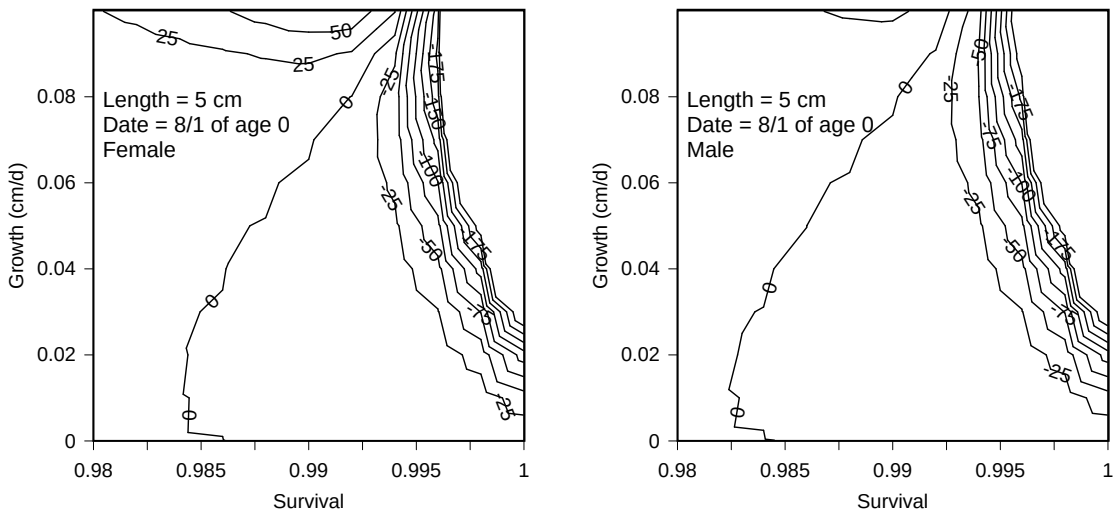

Figure 2. Anadromy benefit contours for 5-cm juveniles at their first August 1. The contoured value is the fitness measure for anadromy F_A minus the fitness measure for residency F_R.; hence, anadromy is chosen in the region with positive values (here, upper left). Juveniles remain residents unless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

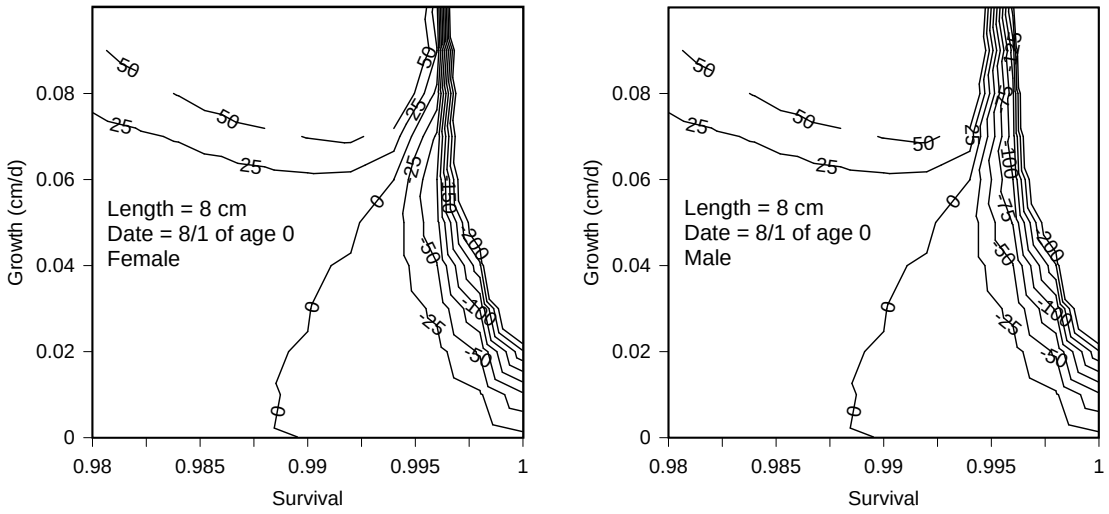

Figure 3. Anadromy benefit contours for 8-cm juveniles at their first August 1. Larger size, compared to Figure 2, increases the regions over which anadromy is chosen.

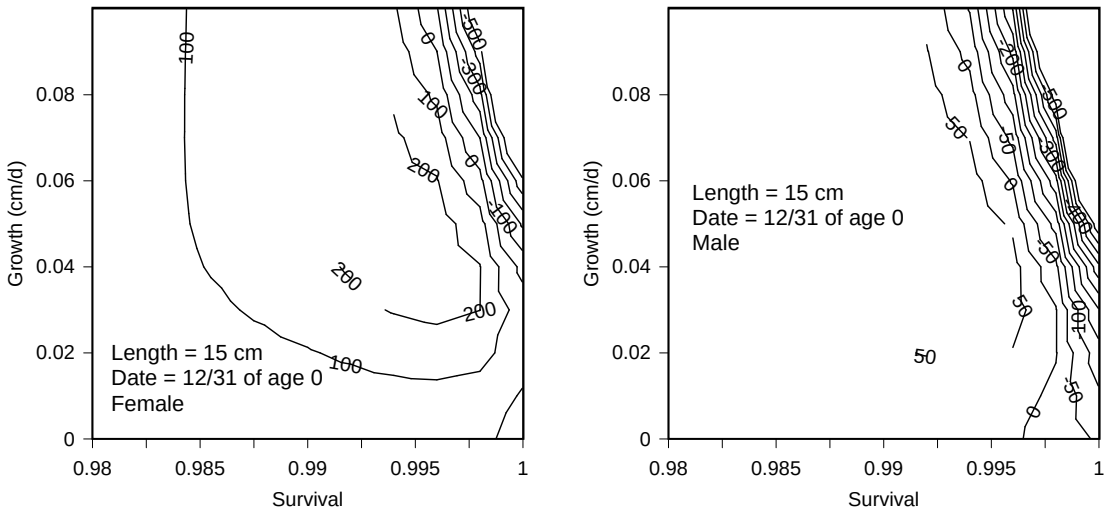

Figure 4. Anadromy benefit contours for 15-cm juveniles at the end of their first year. Residency is only chosen at high growth and survival.

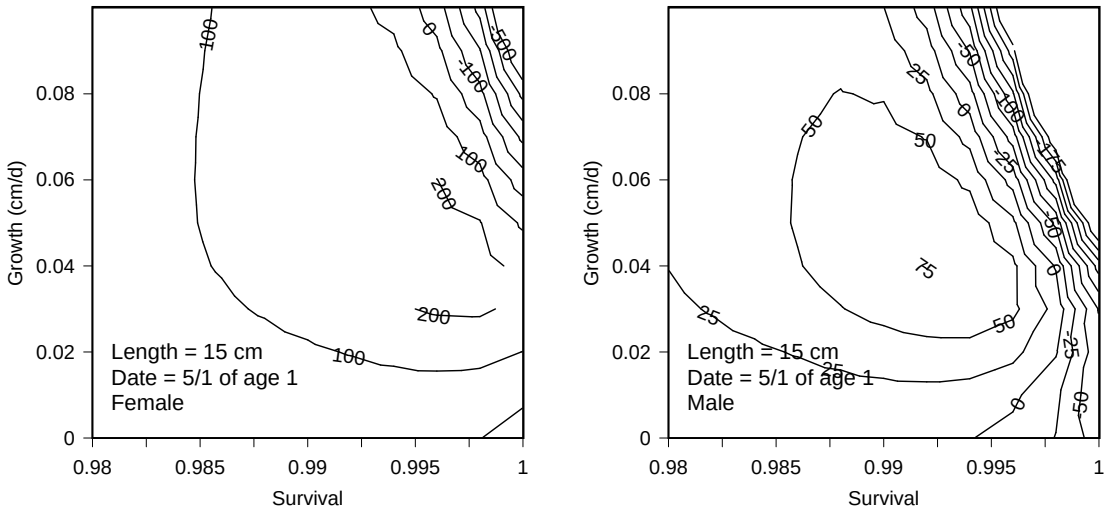

Figure 5. Anadromy benefit contours for juveniles at the May 1 of their second year, length = 15 cm. Clearer differences between males and females are apparent, with males choosing residency over a wide range.

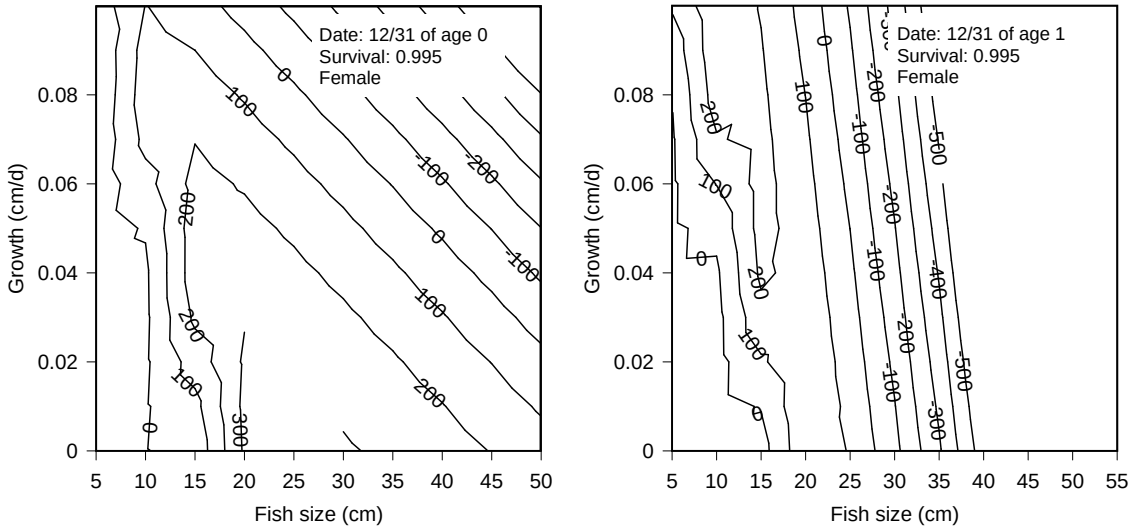

Figure 6. Growth-size contours for comparison to figures 5(A, C) and 7(A, C) of Satterthwaite et al. (2010).

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 for steelhead.
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 for steelhead.
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	30.0	Rainbow trout values from Railsback et al. (2009).
mortReddHiTT9	21.0	
mortReddLoTT1	-3.0	
mortReddLoTT9	0.0	
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.

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3 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.

3.1 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 7). With very simple changes, additional species or races of both types can be added to the code.

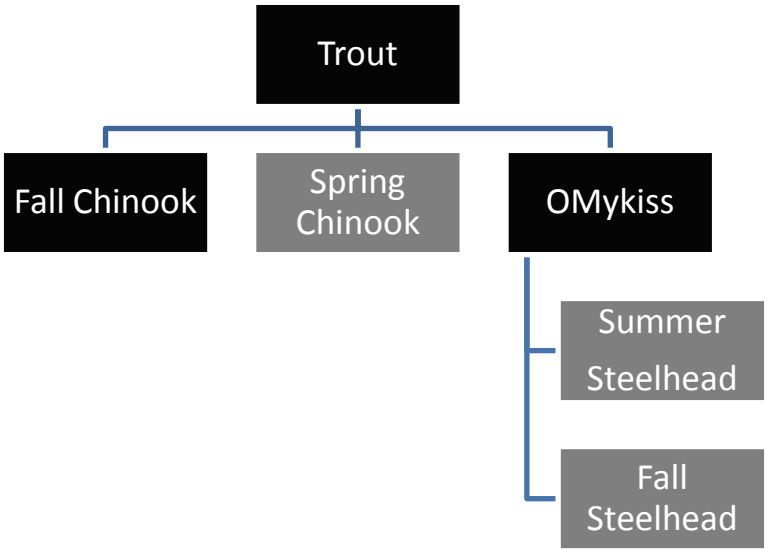

Figure 7. Class diagram for inSALMO-FA model code: each box represents an Objective-C class that models a salmonid species or race. Classes are subclasses of the class above them. Black boxes represent classes in the steelhead version of inSALMO-FA and grey boxes represent hypothetical subclasses that could be added to model additional fish species.

3.2 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.

3.3 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.)

4 inSALMO Model Description: Objectives and Overview

4.1 Document Objectives

This document describes version 1.5 of *inSALMO*, an individual-based salmon population model. Versions 1.0 and higher of *inSALMO* are focused on the effects of reservoir and river management alternatives on freshwater life stages: spawning, redd incubation, and juvenile rearing and outmigration. These versions were developed by Lang, Railsback and Associates (LRA) and USDA Forest Service, Pacific Southwest Research Station, for the US Bureau of Reclamation and US Fish and Wildlife Service.

This document is prepared primarily as a model description help file to be packaged with the *inSALMO* software. It contains a complete description of the model's assumptions, methods, and parameters; and their basis. Additional information on the background, history, application, and software of *inSALMO* is available in the project report (Railsback et al. 2011), to which this is an appendix.

4.2 Overview of *inSALMO* 1.5

Version 1.5 is an update and revision of version 1.0[2]. It was developed as a product of model validation and testing conducted for the US Fish and Wildlife Service in 2012-13. This report was developed by revising the relevant parts of the *inSALMO* 1.0 model description. Revisions made as part of this update are identified in this report via footnotes.

inSALMO 1.0 represents three life stages of salmon and the stream habitat they occupy. This section very briefly summarizes the kinds of things in the model and the actions they execute. Complete detail is provided in later sections.

Habitat is represented as one or more "reaches" of stream spawning and rearing habitat. Each reach is made up of a collection of polygonal cells. Flow, temperature, and turbidity are characteristics of reaches, whereas depth and velocity vary among cells. Cells can be either irregular or rectangular, depending on what kind of hydraulic model is used (Figure 8). There are no restrictions on how many cells can be in a reach, how many reaches can be in a model, or how multiple reaches are arranged spatially.

The three salmon life stages in the model are spawners, redds, and pre-smolt juveniles. Model runs start with adult salmon arriving in the reaches ready to spawn. Female spawners select a spawning cell and create a redd, then defend the redd from superimposition until they die. Redds are simulated as individual objects, with the number of live eggs in each possibly being decreased by a variety of mortality sources. Redd development status is a function of water temperature. When redds are fully developed, one new juvenile is created for each surviving egg. The model can simulate multiple races and species of salmon, though its primary application has been to fall-run Chinook.

Juvenile salmon have three behaviors: selecting habitat, feeding and growing, and surviving or dying. They select habitat cells to provide a good tradeoff between growth and survival of

[2] The software corresponding to *inSALMO* 1.0 prior to the v. 1.5 updates was tagged in its repository as version 1.2, 16 April 2013. https://github.com/colinsheppard/insalmo/tree/v1.2.

predation. If none of the cells they can choose among provide a good tradeoff, they can migrate downstream; the rate of downstream migration increases with juvenile size. The model's primary result is the number, timing, and size of juveniles at the time they migrate downstream out of the simulated habitat.

The model runs at a one-day time step. Key inputs describe the shape and cover characteristics of the reachs, and daily flow, temperature, and turbidity. Hence, the model is suited for predicting how changes in instream flow and temperature, and habitat restoration projects, affect spawning success.

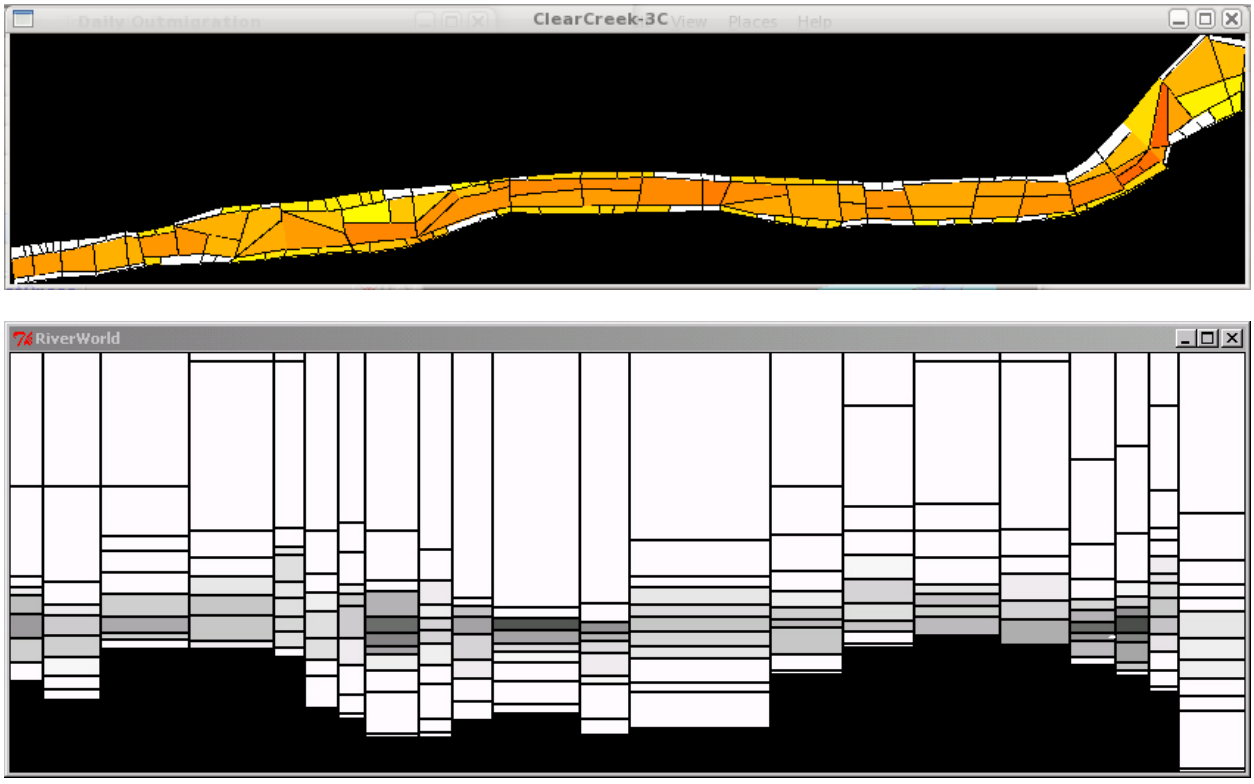

Figure 8. Representations of space in *inSALMO* 1.0. Top: polygonal cells generated in a geographic information system (GIS) or two-dimensional hydrodynamic model. Bottom: rectangular cells from a pseudo-two-dimensional hydraulic model. These are each a plan (top-down) view of one reach.

5 inSALMO Model Description: Terminology and Conventions

This section describes the terms and modeling conventions followed in this document and in the *inSALMO* software.

5.1 Terminology

The following terms are used as defined here throughout this document. Much of the terminology is taken from Grimm and Railsback (2005).

Action. An element in an IBM's **schedule**. An action is defined by a list of model **objects**, the **methods** of these objects executed by the action (e.g., **traits** of fish, updating the habitat cells; producing output), and the order in which the objects are processed.

Adult. Simulated salmon that have returned from the ocean to their spawning areas ready to spawn. **Spawners** are synonymous with adults.

Behavior, individual behavior, system behavior. What a model fish or fish population actually does during a simulation. A behavior is an outcome of an IBM and the ***traits*** of its individuals.

Cell. The basic unit of habitat in *inSALMO*; habitat conditions vary among cells, but not within a cell.

Data. Input that describes the habitat and fish population to be simulated. Data for *inSALMO* Version 4 includes daily time series of flow, temperature, and turbidity; cell dimensions and state variables; the relations between flow and depth and velocity for each cell; and the characteristics of the initial fish population.

Habitat selection. The **behavior** and corresponding **trait** for selecting which **cell** to feed in each day.

Input. Any of the **data** and **parameter** values that a user provides to *inSALMO* to define a **scenario**.

Method. In object-oriented software, a block of code that executes one particular **trait** or process. Methods are similar to subroutines in non-object-oriented software.

Mortality source. A natural process (e.g., starvation, predation) that causes fish or eggs to die. Mortality sources are modeled as **survival probabilities**.

Object. Something that is represented as a discrete entity with its own state variables. Example objects include individual fish, redds, and cells; and (in the software) observer tools such as graphics windows and the devices that produce output files.

Observation, observer tools. The process of collecting data and information from the IBM; typical observations include graphical display of patterns over space and time and file output of summary statistics. Observer tools are software tools such as graphical user interfaces that make certain kinds of observation possible.

Parameter. A user-specified coefficient for one of the equations used to define traits of fish and habitat. Parameter values are one of several kinds of **input**. Compare to **variable**. Parameter values are ideally developed from empirical literature or field data. A few parameters are best evaluated via calibration.

Population. All the model fish in a simulation. (Or, for simulations with multiple species, all the model fish of a species.)

Reach. *inSALMO* models salmon spawning in one or several reaches. Each reach is a continuous section of a stream or river channel. The habitat within a reach is broken into **cells**.

Replicates. Multiple models runs that represent the same **scenario** but use different pseudo-random number sequences. Replicates are useful for evaluating how much of the variation in results is due to stochasticity.

Scenario. A single, complete set of **input** to *inSALMO*, representing one particular set of environmental conditions or one management alternative. Effects of alternative environmental conditions or management alternatives are typically assessed by comparing output produced by several different scenarios.

Schedule. A description of the order in which events are assumed to occur: the schedule defines the **actions** and the rules for executing them. In an IBM's software, the schedule is the code which defines actions and controls when they are executed.

Spawner. An **adult**.

Survival probability. A model of a **mortality source**. This term refers to a fish's probability of surviving a particular kind of mortality for one day; but it also refers to the methods used to calculate that probability.

State, state variable. A measure of the status of some part of a model (individuals, habitat cells, the population) that typically can be described using a single number. A state variable is a model variable describing a particular state of some model component. State variables may be constant over time and read from input **data**, or may be updated over time by model calculations. Example fish states are weight, sex, and location; cell state variables include distance to hiding cover (a constant input) and food availability (which varies daily); example system states are population biomass, number of species, and mortality rate (number of individuals dying per time step).

Submodel. A part of an IBM's **formulation** that represents one **trait** or process. Dividing *inSALMO* into submodels allows each process to be modeled, calibrated, and tested separately.

Trait. A model of a particular **behavior** of individual fish. A trait is a set of rules for what individuals do at particular times or in response to specific situations in the IBM.

Variable. Any number used in calculations. A variable may be a **parameter** or a **state variable**, or may be a temporary internal variable.

5.2 Conventions

5.2.1 Measurement units

The *inSALMO* formulation and software consistently use these measurement units.

Distance and length are in centimeters (cm), and, therefore, areas are in cm^2, volumes in cm^3, and velocities are in cm per second (cm/s). There are two important exceptions to this

convention. Stream flow is in units of cubic meters per second (m^3/s) because cm^3/s is an unfamiliar and cumbersome measure of stream flow. Habitat input files that define the size and location of cells use distances in meters (m) for convenience. However, all internal variables and outputs involving depth, velocity, area, or distance use length units of cm.

Weight is in grams (g).

Temperature is in Centigrade (°C).

Turbidity is in nephelometric turbidity units (NTU).

Time is in days (d), because the model uses a daily time step. However, there are several exceptions to this convention. Flow and velocity variables are per second. Food availability and intake calculations use hourly rates because the number of hours per day that fish feed is variable.

Fish lengths are fork lengths.

Fish and prey (food) weight variables use wet weight.

5.2.2 Parameter and variable names

The model's formulation uses the parameter and variable naming conventions of the Swarm software used to code the model. This convention has two benefits. First, the variable and parameter names in the formulation document can be the same as in the software. Second, the names are long and descriptive, making it easier to identify exactly what each variable is.

Variable and parameter names typically are made by joining several words. The first word starts with a lower-case letter, and capital letters are used at the start of each subsequent word (e.g., *fishWeightParamA*). Input parameter names start with the kind of object that uses the parameter. These objects include fish, redds, habitat cells, fish mortality sources, and redd mortality sources. Consequently, most parameters start with the words *fish*, *redd*, *cell*, *hab*, *mortFish*, or *mortRedd*. This convention is not strictly followed for variables calculated internally by the model.

Whereas the traditional way of depicting a fish's length-weight relationship is:

$$W = a_L L^{b_L},$$

the same relationship appears in this formulation as:

$$fishWeight = fishWeightParamA \times \left(fishLength \right)^{fishWeightParamB}$$

and the corresponding program statement in the software is:

```
fishWeight = fishWeightParamA * pow(fishLength, fishWeightParamB);
```

5.2.3 Survival probabilities and mortality sources

A number of factors can cause fish or fish eggs to die in *inSALMO*. These factors are referred to as "mortality sources". Although the word "mortality" is used in parameter names and our text, all mortality-related calculations are based on survival probabilities. A survival probability is the (unitless) probability of surviving a particular mortality source for one day. (The term "mortality risk" is commonly used to mean the daily probability of dying, equal to one minus the survival probability.)

Modeling mortality as a survival probability simplifies computations and reduces the chances of error. The probability of surviving several mortality sources is calculated simply by multiplying the individual survival probabilities together. Likewise, the probability of surviving one kind of mortality for *n* days can be calculated by raising the daily survival probability to the power *n*.

5.2.4 Dates

This model uses date input in the "MM/DD/YYYY" format (e.g.: 12/07/1999). The software converts this input to the computer operating system's internal date format that automatically accounts for leap years. All input data and simulations, therefore, include leap days.

Parameters that are days of the year (e.g., spawning is allowed to occur between April 1 and May 31 of each year) are input in the "MM/DD" day format.

5.2.5 Fish ages and age classes

inSALMO uses the convention that fish are age 0 when born and the age of all fish is incremented each January 1. (However, if a simulation starts on January 1 the birthday is skipped.) Fish are assigned to age classes, which are used to define the initial population at the start of a model run and to report simulation results. However, adult age has no effect in version 1.0 of *inSALMO* so, by convention, all adults are simply given an age of 5.

Seven age classes are used (although the number of classes can be changed via relatively simple modifications to the software):

- Age 0—fish that have not yet reached their first January 1.
- Age 1—fish that have survived one January 1.
- Age 2-Age5—fish that have survived the January 1 of two (etc.) years.
- Age 6+—any fish older than Age 5.

5.2.6 Habitat dimensions and distances

X and Y dimensions. Version 1.0 of *inSALMO* uses a general two-dimensional format for depicting space. Cells can have 3 or more sides. Velocities are modeled only as magnitudes without any direction. The X and Y coordinates used to define cell corners can be in any rectangular coordinate system. On *inSALMO*'s graphical displays of the stream, the X coordinate is the horizontal dimension and increases from left to right; Y is the vertical dimension and increases from bottom to top. Hence, input in standard coordinate systems such as UTM appear with north on the top and east to the right.

Distances between cells. Some calculations in the model require values for the distance between two cells (e.g., for finding all the cells within a fish's maximum movement distance). The distance between two cells is calculated as the straight-line distance between the centroids of the cells.

5.2.7 Logistic functions

The survival probabilities make extensive use of logistic functions, which are useful for depicting many functions that vary between 0 and 1 in a nonlinear way. The Y value of a logistic function increases from zero to one, or decreases from one to zero, as the X value increases over any range. In inSALMO, logistic functions are defined via parameters that specify two points: the X values at which the Y value equals 0.1 and 0.9. The logistic functions are defined as:

$$S = \exp(Z) \Big/ 1 + \exp(Z)$$

where

$$Z = LogistA + (LogistB \times habitatVariable)$$

$$LogistA = \left(LogistC - LogistD\right) \Big/ \left(habVarAtS01 - habVarAtS09\right)$$

$$LogistB = LogistC - \left(LogistA \times habVarAtS01\right)$$

$$LogistC = \ln\left(0.1 \Big/ 0.9\right)$$

$$LogistD = \ln\left(0.9 \Big/ 0.1\right).$$

These equations evaluate the example survival probability *S*, given the X value *habitatVariable*. The parameters *habVarAtS01* and *habVarAtS09* are the values of the habitat variable at which survival is defined to be 0.1 and 0.9, respectively. The two X value parameters (*habVarAtS01* and *habVarAtS09* in this example) must not be equal. (Many examples of logistic functions are shown graphically in Section 7.4.)

6 inSALMO Model Description: Habitat

Habitat is depicted in *inSALMO* at three scales. The entire model is represented as a network of reaches (but just one reach can be used). Reaches are habitat objects representing a whole river or stream segment, and cells are objects representing the habitat units that salmon occupy. A model contains one or more reaches, and each reach is made up of many cells.

6.1 Reaches

Reaches represent variables and processes that are assumed uniform over a reach. Reaches also keep track of how they are linked to other reaches.

6.1.1 Reach-scale variables

The parameters used to calculate food production in each cell (Section 6.2.6) are assumed uniform over a reach and constant over time. Hence, they are input as reach parameters. Two other reach-level parameters are the maximum flow at which salmon will spawn (Section 7.1.1) and the fraction by which velocities are reduced for salmon swimming in velocity shelters (Section 7.3.7).

Reaches have three variables that are updated daily from input files: daily mean values of flow (m^3/s), temperature (˚C), and turbidity (NTU). Temperature and turbidity are assumed the same for all cells in a reach. Flow is used primarily to determine the depth and velocity in each of the reach's cells (Section 6.2.2).

Flow is also used to calculate the probability of redd scour (Section 8.1.2). Scour is actually a function of peak flow, and peak flows during high-flow events can be significantly higher than daily mean flows. Hence, during peak flow periods that coincide with redd incubation, *inSALMO* may better represent redd scour if daily mean flows are replaced by daily peak flows. This change should have negligible other effects on model results because (unless multiple salmon races are simulated) few fish are present during the incubation period. (Any fish that are present could be affected by the higher velocities resulting from peak vs. mean daily flows.)

The day length (*dayLength*, number of hours of daylight, including twilight) is a calculated reach variable. (The same day length is used for all reaches.) Day length is used to model the time salmon spend feeding (Section 7.3.2) and affects predation mortality (Section 7.4). The value of dayLength is updated daily, using equations modified from the Qual2E water quality model (Brown and Barnwell 1987).

$$dayLength = 24 - 2\left[\left(\frac{12}{\pi}\right)\arccos\left\{\tan\left(\frac{\pi \times siteLatitude}{180}\right)\tan\delta\right\}\right]$$

where:

$$\delta = \left[\left(\frac{23.45}{180}\right)\pi\cos\left\{\left(\frac{2\pi}{365}\right)(173 - julianDate)\right\}\right]$$

and *siteLatitude* is a model parameter set to the study site's latitude (in degrees) and *julianDate* is the Julian date (day of the year, 1-366, calculated internally from the date). This equation works only for the northern hemisphere.

6.1.2 Reach links

Users of *inSALMO* specify the number of reaches and how they are linked. (Often, only one reach is used.) Reaches can be linked in a network of any kind, including a linear sequence (multiple mainstem reaches only), mainstem and tributaries, and distributaries (Figure 9).

The reach network is specified by providing, for each reach, a reach name and junction numbers for the upstream and downstream ends of the reach. The reach name is a character string of up to

30 characters with no spaces. The reach name is used within the software and in output files to label each reach.

For each reach, junction numbers are provided as two reach parameters: *habUpstreamJunctionNumber* and *habDownstreamJunctionNumber*; both are integers. Junction numbers are used only to build the links that define the reach network, so their value can be arbitrary as long as they are consistent among reaches. Any two or more reaches with the same junction number will be linked at that junction. Figure 9 illustrates ways that networks of reaches can be defined, and Table 3 describes how these networks are defined using junction numbers.

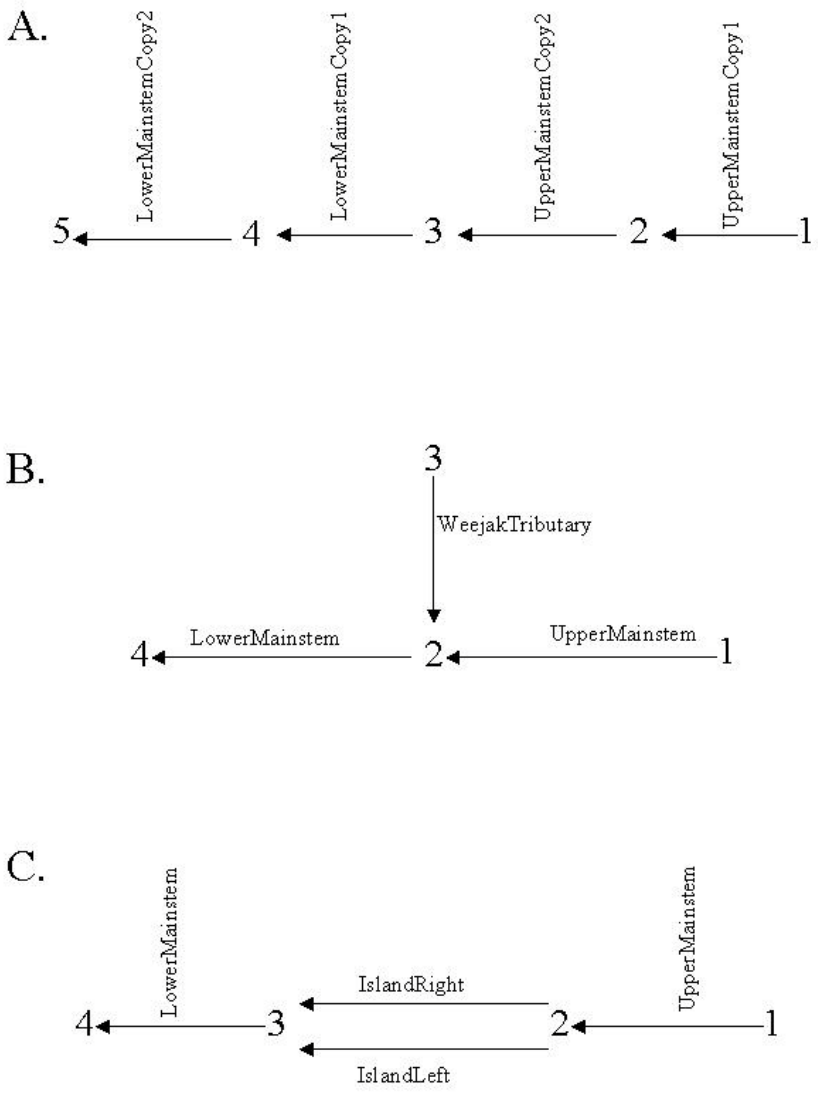

Figure 9. Example reach network configurations, showing junction numbers and reach names. Arrows represent reaches, pointing in the downstream direction. Network A has four sequential reaches generated by using two copies each of an upper and lower study site. Network B has two mainstem reaches and a tributary. Network C has reaches on either side of an island.

Table 3. Junction numbering for the example reach networks.

Network	Reach name	Upstream junction number	Downstream junction number
A	UpperMainstemCopy1	1	2
	UpperMainstemCopy2	2	3
	LowerMainstemCopy1	3	4
	LowerMainstemCopy2	4	5
B	UpperMainstem	1	2
	LowerMainstem	2	4
	WeejakTributary	3	2
C	UpperMainstem	1	2
	IslandLeft	2	3
	IslandRight	2	3
	LowerMainstem	3	4

6.2 Cells

6.2.1 Cell boundaries and dimensions

Cells are depicted as polygons with three or more sides. A reach's cells can be laid out using GIS software, or as the mesh of a hydraulic model—either a pseudo-two-dimensional model such as those of PHABSIM or a fully two-dimensional hydrodynamic model. *inSALMO* imports the corner coordinates of each cell. Any space not within a cell is treated as unavailable to the model fish.

Cells also have a variable *cellReachEnd* that simply holds a static value indicating whether the cell is at the upstream end (*cellReachEnd* = "U") or downstream end ("D") of their reach, or not at an end ("I"). These variables are used by fish in determining which cells of which reaches they potentially could move to (Section 7.2.2.2). The values of *cellReachEnd* are determined by the model user and read in as input. Cells should have *cellReachEnd* equal to "U" or "D" only if they are at the end of their reach *and* are wet at typical base flows.

6.2.2 Depth and velocity

The depth and velocity of each cell (and the number of cells that are submerged and therefore available to salmon) vary with the daily reach flow. A cell's water velocity is treated as a magnitude: the mean speed of the water without regard to direction.

To take advantage of existing stream hydraulic modeling software and avoid having to include hydraulic simulations, *inSALMO* imports lookup tables of water depth and velocity, as a function of flow, for each cell. This approach allows all the hydraulic model building, testing, and calibration to be conducted in existing, specialized hydraulic software and manipulated, if necessary, in GIS.

The input depth and velocity lookup tables should contain a wide range of flows. If *inSALMO* 4.5 is used to simulate flows higher than those in the lookup table input it is likely to produce unrealistic depths and velocities for some cells.

An example is depicted graphically in Figure 10. In this example, the cell is dry (depth and velocity are zero) at flows up to 20 m^3/s. As flow increases, depth increases steadily. Velocity at this example cell, however, does not increase monotonically with flow: it increases rapidly with flows between 25 and 30, then drops off, then increases sharply at flows around 85. Such discontinuities in how velocity increases with flow in part an artifact of how the hydraulic simulations were done (three hydraulic model calibrations were used for low, middle, and high ranges of flow) but also reflect the discontinuities that really occur in rivers. Because of eddies and other hydraulic complexities, it is not unusual for velocity to decrease in a cell as flow increases over some ranges. (This example is slightly atypical: velocity does increase monotonically with flow at most cells. However, exceptions like this are common; the example is presented to reinforce that capturing natural hydraulic complexity should be the highest priority in hydraulic simulation.)

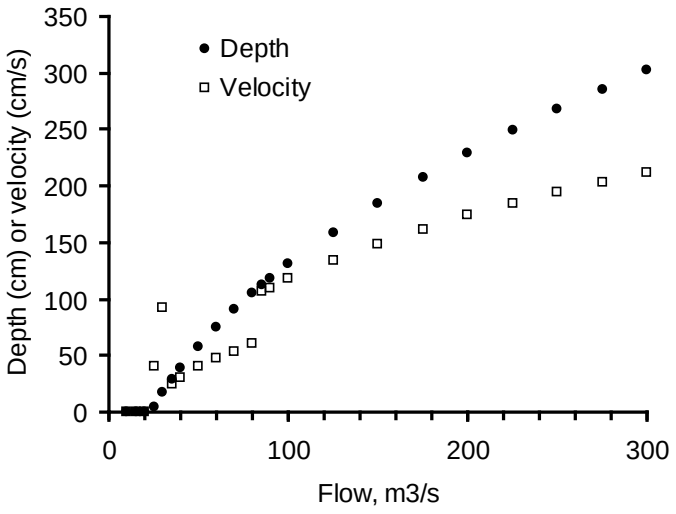

Figure 10. Example depth and velocity input for a cell. Each point represents an entry in the water surface elevation and velocity lookup table that is input for the cell.

On each simulation day, the depth and velocity of each cell are interpolated from the reach's daily flow, using the lookup tables. Linear interpolation is used, so it is important for the lookup table to include many flows. For flows above the highest in the lookup table, depth and velocity are extrapolated upward from the highest two flows in the table. The need to make these

extrapolations can be avoided by making sure the lookup table includes flows lower and higher than any occurring during a model run.

At flows below the lowest in the lookup table, depth is extrapolated downwards from the lowest two values in the table; any negative results are set to zero depth. Velocity is interpolated in this case between zero and the velocity at the lowest flow in the table. Any channel margin cells that are submerged only at the highest flow in the lookup table can have unrealistically high velocities at flows above the highest lookup table flow. Cells that are submerged only at flows above the highest lookup table flows will never have non-zero depth and velocity (because all values in their lookup table are zero).

6.2.3 Velocity shelter availability

The availability of velocity shelters (which affect growth, Section 7.3.7; and high velocity mortality, Section 7.4.2) is modeled by assuming that a constant (over time) fraction of each cell's area provides velocity shelter. This fraction is provided as input (variable *cellFracShelter*, a dimensionless fraction between zero and one). These fractions should include any part of the cell with complex hydraulics that could be used by salmon to reduce their swimming speed while drift feeding. Velocity shelters can be provided by boulders, cobbles or other substrates that induce roughness in the bottom, woody debris, roughness in the banks or bedrock channel, or adjacent cells with near-zero velocities.

In reality, the availability of velocity shelters can vary with a fish's size and the flow; *inSALMO* ignores this variability because of its complexity. Instead, *cellFracShelter* should represent drift feeding habitat for juvenile salmon at a typical base flow.

A cell keeps track of its total velocity shelter area (*cellFracShelter* × *cellArea*) and also keeps track, over time, of how much of that shelter area is occupied by fish. Each fish using velocity shelter in a cell occupies an area of shelter equal to the square of the fish's length (Section 7.3.7). A fish has access to shelter if the total shelter area of its cell is greater than the shelter area already occupied by more dominant fish. This means that a fish has access to shelter if there is any unused shelter space available for it in the cell. (Competition for food, not velocity shelter space, is more likely to limit the density of fish in a cell.)

6.2.4 Spawning gravel availability

Spawning gravel availability is described as the fraction of cell area with gravel suitable for salmon spawning, assumed to be constant over time. This spawning gravel fraction (variable *cellFracSpawn*, a dimensionless fraction between zero and one) is provided as input for each cell.

6.2.5 Distance to hiding cover

The habitat input variable *cellDistToHide* (m) is an estimate of how far a fish in the cell would have to move to find hiding cover. This variable is used in the terrestrial predation mortality model (Section 7.4.5). The kind of habitat that salmon can use for hiding varies with fish size. Because the focus of *inSALMO* is on juvenile rearing, the terrestrial predation formulation is designed so that *cellDistToHide* should represent hiding for juveniles.

6.2.6 Food production and availability

The amount of food available to fish is a very important habitat variable, probably more important than flow or temperature in determining fish population abundance and production except under extreme conditions. Unfortunately, the processes influencing food availability for stream salmonids are complex and not well understood. Although some studies (Gowan and Fausch 2002, Morin and Dumont 1994, Railsback and Rose 1999) indicate that food availability and consumption can vary with factors including flow, temperature, fish abundance, and physical habitat characteristics, there is little information available on how food availability varies over time and space at scales relevant to individual-based models. Modeling food production is also complicated by the multiple sources of food available to fish. Stream salmonids are commonly observed feeding both by "drift feeding"–maintaining a stationary position and capturing food that drifts past; and by "search feeding"–actively searching for food on the stream bottom or surface. *inSALMO* separately models "drift" food that moves with the current and "search" food that is relatively stationary and must be searched out by the fish. Both drift and search food may originate with benthic production or from terrestrial input.

Because *inSALMO* assumes fish compete for the food available in each cell, cells must keep track of: (a) how much food of each type is produced each day; and (b) how much is available to a particular fish.

6.2.6.1 Production

In the absence of established models of salmon food availability, *inSALMO* uses models that are simple yet mechanistic and easily calibrated using observed salmon growth and survival. Food production is modeled using the simple assumption that (1) the concentration of food items in the drift (*habDriftConc*, grams of prey food per cm^3 of stream volume) and (2) the production of search food items (*habSearchProd*, grams of prey food produced per cm^2 of stream area per hour) are constant over time and space. These two variables are input as habitat parameters.

[How food is produced in specific habitats such as riffles, and depleted by fish as it travels downstream, has been simulated in other models (e.g., Hughes 1992a). However, the model of Hughes (1992a) shows that simulating drift production and depletion over space would require a major increase in the complexity. The simpler approach used in *inSALMO* appears to generally capture the important dynamics of food competition.]

The salmon feeding formulation uses hourly food production and consumption rates because the number of feeding hours per day varies. The hourly food production rates are determined by the physical characteristics of habitat cells. The rate at which search food is produced in a cell (*searchHourlyCellTotal*, g/h) is simply the cell area multiplied by *habSearchProd*.

The rate at which drift food is produced in a cell (*driftHourlyCellTotal*, g/h) is modeled as the rate at which prey items flow into the cell from upstream, plus the rate at which consumed prey are regenerated within the cell:

$$driftHourlyCellTotal = 3600 \times cellArea \times cellDepth \times cellVelocity \times habDriftConc / habDriftRegenDist.$$

The constant 3600 converts the rate from per second to per hour. The *habDriftRegenDist* term has two purposes. First, it simulates the regeneration of prey consumed by drift-feeding fish. Second, it makes the amount of drift food available per cell area independent of the cell's shape. Without this term, five cells 2 m in length (in the upstream-downstream direction) would have five times the food availability of one 10 m-long cell.

The parameter *habDriftRegenDist* (cm) should theoretically have a value approximating the distance over which drift depleted by foraging fish is regenerated. Smaller values of *habDriftRegenDist* provide higher production of food in a cell. This parameter can be used to calibrate habitat selection and survival of starvation; varying it changes drift food availability without changing the amount that a drift-feeding fish captures. The parameter *habDriftConc* also affects the amount of food in a cell, but unlike *habDriftRegenDist*, also affects food capture rates of drift-feeding fish (Section 7.3.3).

6.2.6.2 Availability

The amount of food available to a particular salmon affects the salmon's habitat selection and growth methods (Section 7.2.1). Food availability to a fish is modeled as the hourly rate at which food is produced but not consumed by larger fish, so is still available for other fish. Availability is tracked separately for drift and search food; these rates are *driftHourlyCellAvail* (g/h) and *searchHourlyCellAvail* (g/h). For example, a cell's drift food may be completely consumed by larger fish (*driftHourlyCellAvail* is zero) while all of its search food remains available for any fish that chooses to use search feeding (*searchHourlyCellAvail* equals *searchHourlyCellTotal*).

The cells keep track of drift and search food availability. At the start of a simulation day, *driftHourlyCellAvail* is set equal to *driftHourlyCellTotal* and *searchHourlyCellAvail* is set equal to *searchHourlyCellTotal*. As the salmon execute their habitat selection methods (Section 7.2), the rate of drift or search food consumed by any fish choosing to occupy the cell is subtracted from the food availability rate for additional fish. When a fish's consumption is limited by the amount of food available in the cell, its consumption will equal all the remaining availability and no food will be available for additional fish. Any fish moving into a cell where all the (drift or search) food is consumed by larger fish will consequently have zero (drift or search) food available for it to consume.

7 inSALMO Model Description: Fish

This section describes the methods used by the fish objects in *inSALMO*. These fish objects represent two of the three salmon life stages in the model; the other life stage—incubating eggs and alevins—are represented by redd objects (Section 8). With some key exceptions, both adult spawners and juvenile salmon use the same methods and parameters.

Fish daily carry out four sets of actions: spawn, select a habitat cell, feed and grow, and survive or die according to survival probabilities that vary with habitat cell and fish characteristics. The methods used in these actions are described in this section. The schedule for fish actions—the order in which they are executed—is summarized in Section 11.2.

Some of the parameters used in fish methods are clearly species-specific or site-specific. Example values for these parameters are provided here, along with information on the species, races, or sites for which they were developed. Many parameter values, however, can be

considered acceptable for stream salmonids in general: whatever variation there may be in parameter values among species is expected to be unimportant compared to other variability and uncertainty in the method the parameter is used in.

7.1 Spawning

The formulation for when and where adults spawn is guided by several ideas. First, for *inSALMO*'s purposes as a river management tool it is important to simulate when and where, at a reach and cell scale, salmon spawn. Secondly though the model's purposes do not clearly require representation of spawning decisions as complex adaptive behaviors. Salmonids are clearly capable of adapting some of their reproductive behaviors to environmental conditions and their own state, especially by deciding whether or when to spawn each year considering their current size and condition and habitat conditions (e.g., Nelson et al. 1987). However, *inSALMO*'s objectives do not justify a detailed representation of such processes as the bioenergetics of spawning or the adaptive decision of whether to spawn each year considering the fish's current state and expected growth and mortality risks. Instead, *inSALMO*'s spawning methods simply force model salmon to reproduce general spawning behaviors observed in real salmon. Behaviors are included only if they appear important for simulating effects of physical habitat, flow, and temperature effects on reproduction.

Spawning simulations include five steps: females decide whether to spawn, select a cell to spawn in, create a redd, and identify a male mate; then, both females and males incur a weight loss.

7.1.1 Decide when to spawn

Each day, each female spawner salmon determines whether it meets all of the fish- and habitat-based spawning criteria described below. These spawning criteria restrict spawning to physical conditions (dates, flows, temperatures) when spawning has been observed in real salmon, presumably because spawning is more likely to be successful during those conditions. The criteria for readiness to spawn do not include a requirement that good spawning habitat be available; it is assumed that salmon will spawn whether or not ideal gravel spawning habitat is present, because model input should create spawners only in reaches where they are known to spawn (Section 9.2).

On the days when all the spawning criteria are met for a female, then whether it actually spawns that day is determined stochastically. The probability of spawning on any such day is the parameter *fishSpawnProb* (unitless). This stochastic selection of spawning date imposes some variability in when individual fish spawn; the appropriate degree of variability can depend on what salmon race is being modeled and how much time typically passes between when they arrive at a site and when they spawn. Fall-run chinook typically spawn soon after arriving in their spawning reach, so *fishSpawnProb* should have a relatively high value. Values of *fishSpawnProb* of 0.1, 0.2, 0.3, and 0.4 result in half the adults spawning within 7, 4, 2, and 2 days (Figure 11).

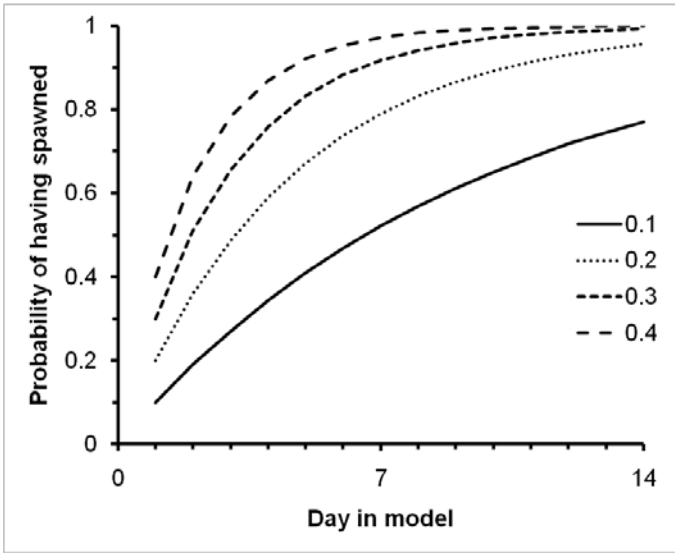

Figure 11. Probability that an adult has spawned vs. how many days it has been in the model, for values of *fishSpawnProb* from 0.1 to 0.4.

7.1.1.1 Not spawned this season

Model salmon cannot spawn more than once. The fish (both males and females) in *inSALMO* have a boolean (yes-no) variable *spawnedThisSeason*. When adults are created, their value of *spawnedThisSeason* is set to NO. If a fish spawns, its value of *spawnedThisSeason* is set to YES. Females are not allowed to spawn if their value of *spawnedThisSeason* is already YES. (If a fish spawns, its value of *spawnedThisSeason* remains YES until spawning season starts again the next year.)

7.1.1.2 Date window

Salmonids generally have distinct annual spawning seasons. This is not surprising because time of year is an important predictor of factors that are critical to successful spawning. For example, early spring spawning may make eggs and fry more vulnerable to cold temperatures or streambed scour from high flows, but spawning too late may make offspring more vulnerable to high temperatures or reduce their ability to compete with earlier-spawned juveniles. Some salmon races migrate to their spawning reaches long before spawning, while others begin spawning as soon as they arrive. Therefore, in *inSALMO* fish can spawn only on days within a user-specified date window.

The date window is specified by two input parameters, *fishSpawnStartDate* and *fishSpawnEndDate*. These parameters are days in MM/DD format. (The spawning window can extend from the end of one year into the next; for example, *fishSpawnStartDate* can be 12/1 with *fishSpawnEndDate* 2/1.)

7.1.1.3 Temperature range

Temperature is widely accepted as a factor controlling the timing of salmonid spawning (e.g., Lam 1988). Temperature could be used by spawners as a cue for seasonal changes and to avoid temperature-induced egg mortality. Therefore, spawning in *inSALMO* can only occur within a

range defined by parameters for maximum (*fishSpawnMaxTemp*) and minimum (*fishSpawnMinTemp*) spawning temperatures for spawning.

7.1.1.4 Flow limit

The maximum flow limit implements the assumption that salmon will not spawn during high flow events. During unusually high flow, cells with depths and velocities suitable for redds (Section 7.1.2) are likely to be along river margins where redds are at risk of dewatering mortality when flows recede; and cells with good habitat for redds at normal flows are vulnerable to scouring. The high flow limit is defined by a single habitat reach parameter, *habMaxSpawnFlow* (m^3/s). A fish is not allowed to spawn if the flow in its reach is greater than *habMaxSpawnFlow*. (This is a habitat parameter instead of a fish parameter because it varies among reaches.) This parameter is highly site-specific and can only be estimated for each study site.

7.1.1.5 Steady flows

Fish are assumed not to spawn when flows are unsteady because flow fluctuations place redds at risk of dewatering or scouring mortality. The parameter *fishSpawnMaxFlowChange* (unitless) is used to define this criterion: if the fractional change in flow from the previous day is greater than the value of *fishSpawnMaxFlowChange* then spawning is not allowed. This fractional change in flow is evaluated as:

$$fracFlowChange = \text{abs}(reachFlow - yesterdaysFlow)/todaysFlow$$

where *reachFlow* is the current day's flow, *yesterdaysFlow* is the flow on the previous day and abs() is the absolute value function. Van Winkle et al. (1996) and Railsback and Harvey (2001) estimated 0.20 as a reasonable value for *fishSpawnMaxFlowChange*.

7.1.1.6 Last spawning date[3]

(Removed.)

7.1.2 Select spawning cell and move there; redd guarding by female spawners

Female spawners select the cell in which they then build a redd. While selection of habitat for foraging is modeled very mechanistically (Section 7.2), selection of spawning habitat is modeled in a simple, empirical way, with spawning cells chosen using preferences for depth, velocity, and substrate observed in real salmon. This decision was made because a detailed, mechanistic representation of spawning habitat selection would require considerable additional complexity: modeling processes such as intergravel flow and water quality, which are extremely data-intensive and uncertain. This additional complexity is not necessary to meet *inSALMO*'s objectives (Section 7.1), but we do need a simple representation of how flow affects where redds are placed because a redd's location affects its survival of dewatering (Section 8.1.1).

[3] This criterion (which forced all spawners to spawn on the last day of the spawning window defined by *fishSpawnEndDate*) was used in versions prior to 1.5 but is removed from *inSALMO* 1.5.

The first step in identifying the location for a new redd is identifying all the cells that are potential spawning sites. This step uses the same method used by salmon to identify potential destination cells during habitat selection (Section 7.2.2), but with two important differences.

The first difference is that a spawner only considers cells within its current reach, even if there are multiple reaches in the model. Without this rule, users would not be able to completely control how many adults spawn in each reach, which is important for testing and using *inSALMO*.

The second difference between habitat selection for spawning vs. foraging represents of redds by female spawners, which is assumed to be an important process controlling the distribution of redds and superimposition mortality for redds. This process is implemented by:

- A fish parameter, *fishSpawnDefenseArea*, represents the area (cm^2) that a female spawner excludes other spawners from as long as she lives (further explained at Section 8.1.5).

- A state variable for cells, *cellAvailableGravelArea* (cm^2) is used to track the area of undefended spawning gravel in each cell.

- Spawners base their selection of spawning cells (below) on *cellAvailableGravelArea* instead of on the cell's total area of gravel.

- During habitat updates at the start of each time step, the value of *cellAvailableGravelArea* is re-set to the cell's total area of spawning gravel minus the value of *fishSpawnDefenseArea* of each live female spawner in the cell (fish in the cell with *spawnedThisSeason* equal to TRUE and sex equal to female; remember that *fishSpawnDefenseArea* can differ among species). However, if the resulting value of *cellAvailableGravelArea* is negative, it is set to zero. This update accounts for spawners who have died and no longer defend their redd.

- Whenever a spawner creates a redd, the value of *fishSpawnDefenseArea* is subtracted from *cellAvailableGravelArea* immediately (before any other spawners select their spawning cell on the same time step). If *cellAvailableGravelArea* becomes negative, it is set to zero.

After potential spawning cells are identified, they are rated by the spawner to identify the cell where the redd will be created. The spawning cell is the potential spawning cell with the highest value of variable *spawnQuality* where:

$$spawnQuality = spawnDepthSuit \times spawnVelocitySuit \times cellAvailableGravelArea.$$

The variables *spawnDepthSuit* and *spawnVelocitySuit* are unitless habitat suitability factors determined using methods described below. (The units of *spawnQuality* are therefore cm^2, but they are unimportant.) The variable *cellAvailableGravelArea* is included in *spawnQuality* because a spawner is assumed more likely to spawn in a cell that has more area of gravel, even if it does not select for bigger patches of gravel. Superimposition redd mortality (Section 8.1.5) is likely to result from this formulation because spawners search many cells for the best spawning

habitat—so it is likely that more than one spawner will use the same cell. However, the best cell for spawning can vary from day to day as flow varies, and due to redd defense.

It is possible that none of the potential spawning cells have a value of *spawnQuality* greater than zero, especially where spawning gravel is extremely sparse. If *spawnQuality* is zero for all potential spawning cells, then the model assumes a spawner will still spawn but ignore gravel area as a criterion. In this situation, the spawner selects the cell with the highest value of *spawnQuality* ignoring spawning gravel:

$$spawnQuality = spawnDepthSuit \times spawnVelocitySuit.$$

If there are still no cells with *spawnQuality* greater than zero, then the spawner places its redd in its current cell. (This condition should occur very rarely, especially if *habMaxSpawnFlow* is well-chosen.)

When the female spawner has selected its spawning cell, the spawner moves to that cell. Male spawners are not assumed to move to the spawning cell.

The suitability factors *spawnDepthSuit* and *spawnVelocitySuit* are unitless variables representing the tendency of salmonids to select fairly well-defined ranges of depth and velocity for spawning (e.g., Knapp and Preisler 1999). Presumably, real salmon select these ranges because they correspond to hydraulic conditions under which egg survival is generally high. For example, intermediate depths have highest suitability, likely because redds placed in shallow water are susceptible to dewatering if flows decline and redds in deep water are more vulnerable to scouring during high flows or siltation during low flows. Intermediate velocities have highest suitability, presumably because low velocities provide inadequate flow of water through the redd (important for providing oxygen and removing wastes) and high velocities present a risk of scouring. Depth and velocity suitability functions are certainly a simplification of how salmonids select spawning habitat, but they are an appropriate simplification for *inSALMO* and available in the literature for a variety of species and sites (e.g., Gard 1997).

The spawning suitability factors for depth and velocity are interpolated linearly from suitability relations provided as parameters. Values of *spawnDepthSuit* are interpolated from the parameters in Table 4 (also plotted in Figure 12). The number of points in this suitability relationship is fixed at five.

Table 4. Spawning depth suitability parameters, with example values for Chinook salmon developed from information in USFWS (2011). The value of *fishSpawnDSuitD1* is a depth; the value of *fishSpawnDSuitS1* is the corresponding suitability value; *fishSpawnDSuitS2* is the suitability for the depth specified by *fishSpawnDSuitD2*, etc.

Parameter Name	Parameter Value (depth, cm)	Parameter Name	Parameter Value (unitless suitability)
fishSpawnDSuitD1	0	*fishSpawnDSuitS1*	0.0
fishSpawnDSuitD2	12	*fishSpawnDSuitS2*	0.0
fishSpawnDSuitD3	27	*fishSpawnDSuitS3*	0.95
fishSpawnDSuitD4	33.5	*fishSpawnDSuitS4*	1.0
fishSpawnDSuitD5	204	*fishSpawnDSuitS5*	0.0

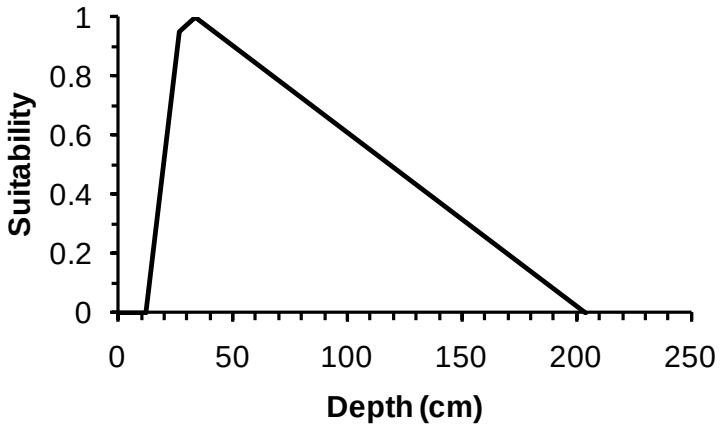

Figure 12. Spawning suitability function for depth from Table 4.

A value of *spawnVelocitySuit* for a cell is interpolated from the six pairs of parameters in Table 5, which includes example parameter values for Chinook. The number of points in this relationship is fixed at six.

Table 5. Spawning velocity suitability parameters, with values for Chinook salmon developed from information in USFWS (2011). The value of *fishSpawnVSuitS1* is the suitability corresponding to the velocity specified by *fishSpawnVSuitV1*, etc.

Parameter Name	Parameter Value (velocity, cm/s)	Parameter Name	Parameter Value (unitless suitability)
fishSpawnVSuitV1	0	*fishSpawnVSuitS1*	0.0
fishSpawnVSuitV2	2.3	*fishSpawnVSuitS2*	0.0
fishSpawnVSuitV3	3.0	*fishSpawnVSuitS3*	0.06
fishSpawnVSuitV4	54	*fishSpawnVSuitS4*	1.0
fishSpawnVSuitV5	61	*fishSpawnVSuitS5*	1.0
fishSpawnVSuitV6	192	*fishSpawnVSuitS6*	0.0

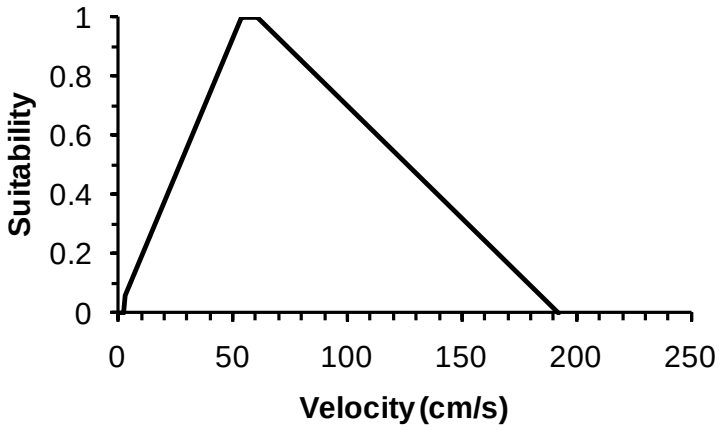

Figure 13. Spawning suitability function for velocity, with values from Table 5.

These example parameter values should be reconsidered for each site that *inSALMO* is applied to. In bigger rivers, for example, greater depths may be suitable without risk of scouring; larger spawners and greater spawning gravel size may reduce the risk of scouring, making higher velocities suitable.

If the model needs to interpolate a value of *spawnDepthSuit* for a depth greater than the value of *fishSpawnDSuitD5* (or a value of *spawnVelocitySuit* for a velocity greater than *fishSpawnVSuitV6*), the value is extrapolated from the last two points in the suitability relation. However, suitability values less than zero are converted to zero. Suitability values greater than one are allowed, so suitability could be scaled from 0 to 10 instead of 0 to 1.0. (It is actually very unlikely that depth and velocity have exactly equal effects on redd location, so they should have different maximum suitability values.)

7.1.3 Create a redd; set number of eggs

When a female spawner has selected a spawning cell, it creates a redd in the cell. The number of eggs in the redd depends on the spawner's fecundity (a function of length) and losses during spawning:

$$numberOfEggs = \left(fishFecundParamA \times fishLength^{fishFecundParamB} \right) \times fishSpawnEggViability$$

The first term in this equation is the spawner's fecundity, the number of eggs it produces. Example values, for Sacramento River Chinook salmon (Table 1 of Healey and Heard 1984, with postorbithypural length converted to fork length) are *fishFecundParamA*: 690 and *fishFecundParamB*: 0.522.

The second term consists of the parameter *fishSpawnEggViability*, which is the fraction of eggs that are successfully fertilized and placed in the redd. (Even though *fishSpawnEggViability* has the same effect mathematically as *fishFecundParamA*, fecundity and egg viability are treated separately to allow clear use of the extensive literature on fecundity.) The number of viable eggs in a redd can be considerably less than the female's fecundity if some eggs are washed away, incompletely buried, or eaten by other fish during redd creation; or if some are not fertilized. This parameter can also be used to represent mortality of eggs and alevins not explicitly included in the model (Section 8.1). There is little published literature to support consistent values of *fishSpawnEggViability* for stream salmonids. For example, Healey (1991) reviewed egg deposition for chinook salmon and found only a few conflicting studies, concluding that egg loss could be high in high-velocity streams but is often low. Anecdotal evidence from salmon and trout in coastal California suggests that the number of emerging eggs often ranges down to 50-60% of the female's fecundity. A value of 0.8 seems reasonable.

7.1.4 Select a male spawner

When a female spawns, it attempts to select a male that also spawns. The only purpose of identifying a male spawner is to impose spawning weight loss (described below) on the male. The selected male spawner is the largest fish in the simulation that meets all the male spawner criteria listed below. The largest eligible male is chosen because larger males are assumed more likely to be sexually mature (Meyer et al. 2003), and more likely to compete successfully to fertilize females (e.g., for Atlantic salmon, Jones and Hutchings 2002).

This selection of a male occurs after the female creates the redd. If several females spawn on the same day, the male selected by the first female spawner becomes ineligible for the subsequent female spawners on the same day (because one of the male spawner criteria is having not previously spawned). If no male meets the criteria as a spawner, there is no effect on the female or redd. The female still produces a fertile redd and incurs weight loss due to spawning. This assumption is made because spawning failure due to absence of males is considered too rare and unpredictable to include in the model. Males are not assumed to move as a result of spawning.

To identify a male spawner (if there is one), a spawning female identifies the largest salmon that:

- Is male;

- Is an adult spawner;
- Is of the same species as the female;
- Occupies the same reach as the female and its new redd; and
- Has not previously spawned during the current spawning season.

7.1.5 Incur weight loss

Spawning involves a significant penalty in body mass and energy, for both males and females. Simulating this loss of mass is how *inSALMO* causes adult salmon to die soon after spawning: the weight loss results in mortality due to starvation and poor condition (Section 7.4.4) soon after spawning (especially because adults are assumed not to eat; Section 7.3). When any model salmon—male or female—spawns, their weight is reduced according to the parameter *fishSpawnWtLossFraction*. Fish weight is multiplied by 1- *fishSpawnWtLossFraction*. A value of 0.4 for *fishSpawnWtLossFraction* is supported by Mesa and Magie (2006).

With the parameters for poor condition survival recommended in Section 7.4.4, a salmon losing 40% of its body mass has a daily survival probability of 0.9. This survival corresponds to a 47% probability of surviving for one week. Survival of adults after spawning affects the model results only via guarding of redds by females (Section 7.1.2).

7.2 Habitat Selection and Outmigration

Habitat selection is the most important trait of juvenile salmon in *inSALMO*. (The word "movement" is commonly also used for this trait; "habitat selection" is a more precise term but in this document the terms are generally interchangeable.) Habitat selection is very important to simulate realistically because it is probably the most important way that stream fish can adapt to short- and mid-term changes in habitat and fish state. Railsback et al. (1999) reviewed methods used in previous models and developed the approach used in *inSALMO*; the approach was then tested by Railsback and Harvey (2002).

The habitat selection trait used by salmon is conceptually simple: every day, each juvenile salmon moves to the habitat cell that (1) is close enough that the fish can be assumed to be aware of conditions in it, and (2) offers the highest "expected fitness". For juveniles, expected fitness is approximated as the expected probability of surviving and reaching reproductive size over a future time horizon. If none of the cells offer expected fitness higher than a size-dependent threshold, the fish migrates downstream out of its current reach. For adults, expected fitness is defined simply as survival until they spawn.

The following subsections explain the habitat selection and outmigration trait in detail.

7.2.1 Competition for resources via dominance hierarchy

The habitat selection trait assumes a size-based dominance hierarchy: fish can only use resources (food and velocity shelters) that have not been consumed by larger fish. Hughes (1992b) showed that stream salmonids rank feeding positions by desirability and the most dominant fish obtain the most desirable sites. Gowan and Fausch (2002) and Hughes (1992b) also showed that dominance is usually, but not always, proportional to length for. The hierarchy is implemented in

inSALMO by executing the habitat selection method in order of descending fish length. The longest individual selects its cell first, and the food and velocity shelter it uses is subtracted from that available in the cell for additional salmon. Subsequent salmon therefore base their habitat selection not on the total resources in each cell but on the resources remaining unconsumed by larger fish.

7.2.2 Identify potential destination cells

When each individual salmon begins its habitat selection method, its first step is to identify the cells that are potential movement destinations. Distance and depth can limit potential destination cells; but the number of fish already in a cell does not limit its availability as a destination.

7.2.2.1 Distance limitation

Only habitat cells within a certain distance are included as potential destinations. This maximum movement distance should be considered the distance over which a fish is likely to know its habitat well enough to be aware when desirable destinations are available, over a daily time step. The maximum movement distance should *not* be considered the maximum distance a fish could swim or migrate in a day.

The maximum movement distance is a function of length. Because mobility and spatial knowledge are assumed to increase rapidly with fish size, this distance is an exponential function. The parameters *fishMoveDistParamA* and *fishMoveDistParamB* are potentially site-specific: fish are likely to explore and be familiar with larger areas in lower-gradient rivers.

$$maxMoveDistance = fishMoveDistParamA \times fishLength^{fishMoveDistParamB}$$

In *inSALMO*, fish can follow a gradient toward better habitat if the gradient is detectable within the *maxMoveDistance*, but they do not have the ability to find and move toward some specific target if that target is beyond *maxMoveDistance*. For example, if habitat generally improves in an upstream direction, fish will have an incentive to gradually move upstream. However, if a very good location for some fish exists farther away than its *maxMoveDistance*, the fish will not be aware of it and try to move to it.

Movement observations from the literature cannot be considered direct measurements of *maxMoveDistance* but can be useful for evaluating its parameters. Observed movement distances in stream salmonids (e.g., Gowan and Fausch 1996, Harvey et al. 1999) show how far fish actually move, not the distance over which they evaluate habitat. These observations are also potentially confounded by a number of factors. Small fish may actually move more than large fish because they are less able to defend a location; this does not mean small fish have a larger maximum movement distance as defined in the model. Movement rates reported in the literature are also potentially deceptive because they are rarely based on continuous or even daily observations of location.

However, literature observations do indicate that stream salmonids commonly select habitat over distances up to several hundred meters. Harvey et al. (1999) showed fall and winter movements of adult (18-24 cm length) cutthroat trout of up to about 55 m in one day in a moderate-gradient stream. Summer conditions (lower flows, higher metabolic rates and food requirements, higher

population densities) may encourage greater movement distances. June (1981) observed little movement in newly emerged cutthroat trout <3 cm; dispersal started after they exceeded 3 cm in length.

Parameter values for a mid-sized, moderate-gradient stream (Table 6) estimate *maxMoveDistance* as 8 m for newly emerged juveniles with length of 4 cm, as 13 m for juveniles 5 cm long, and as 50 m for near-smolts 10 cm long. For adults, with lengths well over 50 cm, this formulation typically means that their entire reach is available for habitat selection.

Table 6. Example parameter values for fish movement distance.

Parameter	Definition	Value
fishMoveDistParamA	Multiplier for maximum movement distance (unitless)	50
fishMoveDistParamB	Exponent for maximum movement distance (unitless)	2

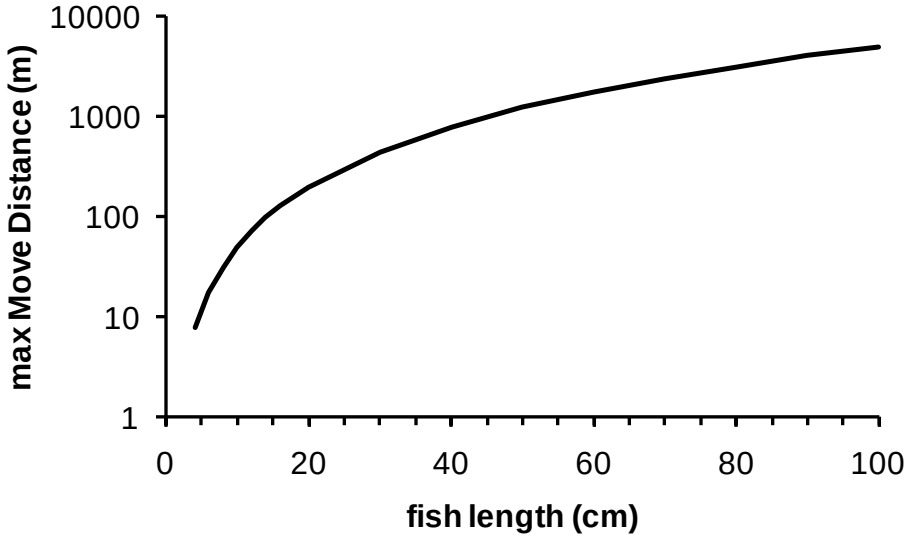

Figure 14. The maximum distance fish can move, as a function of their length, for *fishMoveDistParamA* = 50, *fishMoveDistParamB* = 2.

To identify potential destination cells for habitat selection, a model salmon first calculates its current *maxMoveDistance*. Then all cells in the salmon's reach with distance from the salmon's current cell (as defined in Section 5.2.6) less than *maxMoveDistance* are potential destinations.

7.2.2.2 Cells in other reaches

Adult salmon cannot move to destinations outside the reach they were placed in when the model was initialize (for reasons explained in Section 7.1.2). Juveniles, though, can select habitat in other reaches. If, for example, *maxMoveDistance* for a fish is greater than the distance from the fish's current cell and the downstream end of its reach, and another reach is linked to the

downstream end of the fish's reach, then some cells in the linked reach will be potential movement destinations.

The approach to identifying potential destination cells in adjacent reaches in *inSALMO* 1.0 is very simple: cells at the upstream and downstream ends of each reach are manually identified when habitat input is prepared, and using straight-line distances from cells to the nearest such end cell. Specifically:

- A new static cell variable is added to the input. This variable (*cellReachEnd*) has three possible values: "U" indicates that the cell is on the upstream end of the reach; "D" indicates that the cell is on the downstream end of the reach; and "I" means the cell is intermediate, not at either end. These values are assigned manually (typically, via the GIS) as part of preparing the cell input. Channel margin cells that are at one end of their reach but dry at normal flows can be given a *cellReachEnd* value of "I" to indicate that they should not be used to calculate distance to the end of the reach.

- Cells have two additional static variables that are calculated when the model is initialized. These variables (*cellDistToUS*, *cellDistToDS*) represent the distance from the cell to the upstream and downstream ends of its reach. These variables are simply set to the lowest straight-line distance from the cell's centroid to the centroid of any cell on the upstream and downstream ends of the reach.

- A fish determines whether its potential destination cells include some in other reaches by using *cellDistToUS* and *cellDistToDS*. For example, consider a fish in a reach that has a second reach below it, so that the downstream end of the fish's reach is connected to the upstream end of the other reach. The fish could potentially move into the downstream reach if its cell's value of *cellDistToDS* is less than the fish's value of *maxMoveDistance*. In that case, its potential destination cells would include those in the downstream reach with *cellDistToUS* less than (*maxMoveDistance* minus *cellDistToDS* of the fish's current cell). Potential destination cells are included from all reaches that are attached to the fish's current reach, at an end of that reach within *maxMoveDistance*. (However, a fish cannot move out of one reach, through a second, and into a third reach. Potential destination cells are obtained only from reaches adjacent to the fish's current reach.)

This approach is clearly not exact, especially for sharply curved reaches, but the high uncertainty in the distance over which fish sense and select habitat at a daily time scale makes the error in distance to reach ends unimportant.

For small fish, it is possible that no cells (other than its current one) are closer than *maxMoveDistance*. Having no potential destination cells poses an artificial barrier to movement, an artifact of the model's spatial resolution. This artifact could be important, for example by preventing newly emerged fish from moving from their natal redd to habitat where survival probabilities are higher. In such a situation, competition among newly emerged fish for food would largely be an artifact of the cell's size, which controls how much food is in it. To address this problem, a fish's potential destinations always include the cells adjacent to the fish's current cell. (These adjacent cells are identified as all cells sharing all or part of a side, or a corner, with

the fish's current cell.) Cells from other reaches are not included among the adjacent cells that are always included as potential destinations.

7.2.2.3 Minimum depth

Cells are excluded as destinations if they have depth ≤ 0. Fish are not required to move out of their current cell if its depth drops to zero, but the fitness measure they yse to evaluate potential destinations (Section 7.2.3) provides a strong incentive to move from dry cells. However, if the flow decreases so that the nearest cell with non-zero depth is farther away than a fish's maximum movement distance (not unlikely for very small fish), then the fish can be trapped in a dry cell. (See Section 7.4.3 concerning stranding mortality.)

7.2.3 Evaluate potential destination cells

Separate methods for selecting among the potential destination cells are used for juveniles, adults that have not spawned, and adults that have already spawned.

7.2.3.1 Juveniles

Juveniles select the potential destination cell that provides the highest value of a fitness measure modified from the "expected maturity" measure of Railsback et al. (1999). The fitness measure represents the juvenile's expected success at surviving and growing until it can smolt and go to the ocean. This measure is calculated as:

$$expectedSmoltSuccess = nonstarvSurvival \times starvSurvival \times fracSmoltSize .$$

The variable *nonstarvSurvival* is the calculated probability of survival for all mortality sources except poor condition, over a specified time horizon given by the parameter *fishFitnessHorizon*. This method assumes that fish use a very simple prediction of future survival: that, over the time horizon, the daily survival probability for risks other than poor condition is equal to the current day's risks. The value of *nonstarvSurvival* is calculated as:

$$nonstarvSurvival = \left(S_i \times S_{ii} \times S_{iii} \ldots\right)^{fishFitnessHorizon}$$

where S_i, S_{ii}, S_{iii}, etc. are the daily survival probabilities for all the mortality sources (*i*,*ii*,…), evaluated for the current day, fish, and cell (these probabilities are described in Section 7.4). The value of *nonstarvSurvival* is determined for the fish's size *before* the daily growth that would occur at the potential destination cell; this assumption is made to simplify the model's software.

The formulation of *nonstarvSurvival* implicitly assumes that salmon consider all mortality sources in their habitat selection decision. This means that the salmon are assumed to be aware of all the kinds of mortality in the model and are able to estimate the risk posed by each. This assumption seems reasonable for all the mortality sources currently in *inSALMO*.

In the equation for *expectedSmoltSuccess*, the value of *starvSurvival* is the probability of surviving the risk of poor condition (closely related to starvation; Section 7.4.4) over the number of days specified by the parameter *fishFitnessHorizon*. This term introduces the effects of food intake to the fitness measure. The value of *starvSurvival* is determined by the following steps

(Railsback et al. 1999). The method assumes that fish evaluate *expectedSmoltSuccess* using the simple prediction that the current day's growth rate would persist over the time horizon.

- Determine the foraging strategy, food intake, and growth (g/d) for the fish and habitat cell in question, for the current day, using the methods in Section 7.3.
- Project the fish's weight, length, and condition factor *fishCondition* (Section 7.3.1) that would result if the current day's growth persisted over the fitness time horizon specified by *fishFitnessHorizon*. The daily growth is multiplied by *fishFitnessHorizon* to determine the change in weight over the time horizon; the corresponding change in length and *K* are determined using the methods described in Section 7.3.1.
- Approximate the probability of surviving starvation over the fitness horizon, estimated as as the first moment of the logistic function of poor condition survival vs. *K* (Section 7.4.4):

$$starvSurvival = \left[\frac{1}{a} \ln\left(\frac{1 + e^{(aK_{t+T}+b)}}{1 + e^{(aK_t+b)}} \right) \Big/ (K_{t+T} - K_t) \right]^T$$

where K_t is the fish's value of *fishCondition* at the current day and K_{t+T} is the projected condition factor at the end of the fitness horizon, T is equal to *fishFitnessHorizon*, and a and b are the *logistA* and *logistB* variables (determined within the code from parameter values; see the logistic function conventions described in Section 5.2.7) for poor condition mortality. This equation would cause a divide-by-zero error when K_{t+T} equals K_t, a common condition because K equals 1.0 whenever fish are well-fed. This equation is also subject to significant errors due to the limits of computer precision when K_{t+T} is extremely close to K_t. To avoid these problems, *starvSurvival* is set equal to the daily survival probability for K_t, raised to the power *fishFitnessHorizon*, whenever the difference between K_{t+T} and K_t is less than 0.001.

The final term in the equation for *expectedSmoltSuccess* is *fracSmoltSize*, which represents how close to smolting a juvenile would be at the end of the fitness time horizon. It is simply (a) the length the fish is projected to be at the end of the time horizon, divided by (b) the parameter *fishOutmigrateSuccessL9*, and (c) limited to a maximum value of 1.0. The parameter *fishOutmigrateSuccessL9* represents a length at which outmigration success becomes high (Section 7.2.5).This term gives juvenile salmon an incentive to select cells with higher growth, encouraging them to reach the size necessary for smolting and ocean survival.

The time horizon variable *fishFitnessHorizon* is the number of days over which the terms of the expected smolt success fitness measure equation are evaluated. The biological meaning of this variable is the time horizon over which fish evaluate the tradeoffs between food intake and mortality risks to maximize their probability of surviving and reproducing. It is discussed in the "unified foraging theory" (also called "dynamic state variable modeling" literature; Mangel and Clark 1986, Houston and McNamara 1999, Clark and Mangel 2000). Ideally, fitness is considered a lifetime process, so longer time horizons better reflect how an individual's fitness depends on how well it makes decisions throughout its reproductive life. However, the simple prediction used to evaluate *expectedSmoltSuccess*—that habitat and competitive conditions are

constant over the time horizon—becomes very questionable for long time horizons. Smaller values of *fishFitnessHorizon* place less emphasis on food intake and avoiding starvation in movement decisions. Values of *fishFitnessHorizon* of 5 - 10 d cause *expectedSmoltSuccess* to vary almost exclusively with non-starvation survival, with very little effect of food intake and growth. Values of *fishFitnessHorizon* in the range of 100 d caused *expectedSmoltSuccess* to vary almost exclusively with growth rates when growth was less than the minimum needed to maintain a condition factor of 1.0. A value of 90 d has been successful in several studies validating related decision models (Railsback and Harvey 2002; Railsback et al. 2005).

Adults that have not yet spawned

Adults that have not yet spawned use a habitat decision method similar to that of juveniles but with two key differences. First, adults do not consider as potential destinations any cells outside their current reach, for reason discussed at Section 7.1.2. Second, growth is assumed unimportant to adults so they select a cell that provides the highest value of a fitness measure that considers only survival:

$$expectedSurvival = nonstarvSurvival \times starvSurvival$$

where *nonstarvSurvival* and *starvSurvival* are as defined in Section 7.2.3.1. Hence, adults that have not yet spawned select habitat that provides a combination of safety from predators (e.g., deep cells with hiding cover nearby) and low energetic cost (low velocities or availability of velocity shelter, which reduce swimming metabolism and the risk of poor condition mortality).

7.2.3.2 Spawned adults

After adults have actually spawned, they are assumed to remain in the cell they were in when they spawned. Female spawners actually move to the spawning cell during their spawning action, so they stay in the cell where their redd is (which is essential for making redd defense work; Section 7.1.2). Male spawners do not move to the cell they spawn in, so they remain in the cell they selected on the day they spawned.

7.2.4 Move to best destination and consume its resources

After each fish identifies the cell that has the highest value of its fitness measure, it moves there. When a fish moves into a cell, the resources it uses are subtracted from those available for subsequent fish (sections 6.2.3; 6.2.6). These resources may include one of the two kinds of food, and velocity shelter. Adults are assumed not to consume any food, and spawned adults are assumed not to use any velocity shelter. A fish may move into a cell even when none of these resources remain available to it, in which case its consumption of them is zero.

7.2.5 Outmigration as a habitat selection alternative

Juvenile salmon can “outmigrate”—move downstream toward the ocean—as an alternative to staying in their current reach. Outmigration is often thought of (and modeled, in previous versions of *inSALMO*) as two different processes: voluntary and involuntary. Involuntary outmigration is thought of as the movement downstream, perhaps uncontrolled, of fish that have failed to establish and grow near where they were spawned. These fish may die, or they may end up in downstream habitat with sufficient resources for them to grow and survive. The widely observed downstream movement of moribund fry shortly after emergence is thought of as

involuntary outmigration. Voluntary outmigration is considered the intentional movement toward the ocean of juvenile salmon that are relatively healthy and searching for "bigger" habitat as they grow or are nearing readiness to smolt and enter salt water.

In *inSALMO*, all outmigration is treated as the consequence of one part of the habitat selection decision: fish choose to move downstream if their expectation of success downstream is greater than their expected success in their current reach. Fish therefore decide to migrate out if they are either (a) doing poorly so expected success if they stay is low, or (b) approaching smolt size so their expected success if they outmigrate is high. This approach requires a definition of expected success at the current reach and expected success for downstream migration, and specification of how juveniles move downstream when they do.

Expected success in current reach. The measure of success in the fish's current reach is simply its "expected smolt success" (the variable *expectedSmoltSuccess*; Section 7.2.3.1) at the best cell it considers as a habitat selection alternative. (This cell could be in a different reach than where the fish is when making its decision.)

Expected success downstream. The model of a fish's expected reproductive success if it migrates downstream is a simple logistic function of the fish's length. This "outmigration success" function (Figure 15) is not a model of how likely the fish is to survive to adulthood and reproduce but instead a model of the *relative* likelihood of eventual reproductive success compared to the alternative of staying in the best cell available to it. The logistic form and parameters of this function are based on the assumption that the probability of a smolt returning to spawn increases sharply with the length at which it smolts, over a range of approximately 5-12 cm, but is little affected by smolt size above that range. A second basis for the logistic function is the assumption that increasing size increases the probability that a downstream migrant can find and exploit profitable habitat while reducing the probability of predation by other fish.

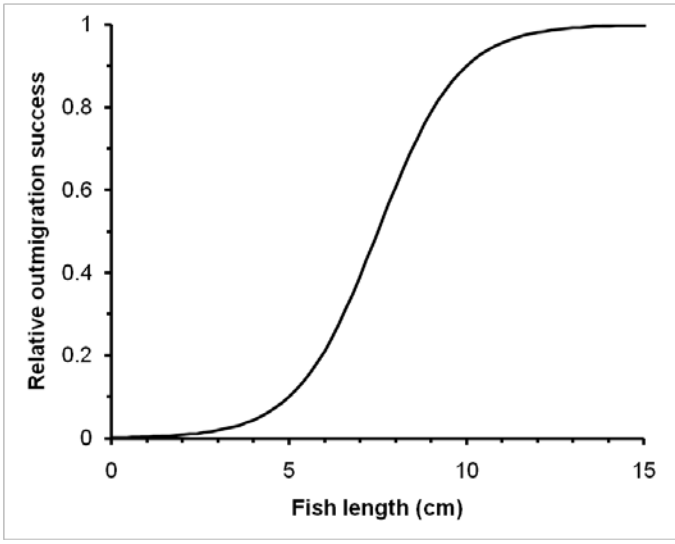

Figure 15. The outmigration success function of fish length, with *fishOutmigrateSuccessL1* and *fishOutmigrateSuccessL9* set to 5.0 and 10.0 cm.

The outmigration success function is defined by two new fish parameters: *fishOutmigrateSuccessL1* and *fishOutmigrateSuccessL9*. These are, respectively, the lengths (cm) at which the function has values of 0.1 and 0.9.

Outmigration movement. When a fish chooses to migrate downstream, it moves, on the current day, to the next-downstream reach if there is one. Upon arriving at that reach, the fish repeats its habitat selection action to find a good cell in that reach. Juvenile salmon are allowed to move downstream at most one reach per day.[4] If there is no model reach downstream of its current one, the fish is treated as an outmigrant from the model.

To provide complete detail, the following steps implement outmigration as part of habitat selection.

- The fish executes habitat selection as described in Section 7.2.3.1, calculating *expectedSmoltSuccess* for each potential destination cell and identifying the cell with highest *expectedSmoltSuccess*.

- The fish then evaluates the logistic outmigration success function for its current length.

- If *expectedSmoltSuccess* for the best cell is greater or equal to the outmigration success function value, the fish moves to that cell (Section 7.2.4).

- If instead *expectedSmoltSuccess* for the best cell is less than the outmigration success function, the fish migrates downstream by:

    - 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 described in Section 7.2.6.

    - 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 juvenile's maximum sustainable swimming speed (Section 7.4.2). This swimming speed depends on temperature, which can vary among reaches; here, it is calculated using the temperature of the juvenile's starting reach, not of the downstream one it is migrating into.[5]

    - If the downstream reach(s) have no cells meeting the depth and velocity criteria, remaining in the best available cell of its current reach instead of migrating downstream. (In this unexpected event, the code issues a warning statement. If this condition persists for days, juveniles could be trapped and unable to migrate downstream.)

[4] The limit of migrating only one reach per day is new to Version 1.5.
[5] The velocity criterion is new to Version 1.5.

- If the downstream reach(s) do have cells meeting thedepth and velocity criteria, moving to randomly selected one of them, removing itself from its current cell.

- Repeating the entire habitat selection action, except that downstream migration is not allowed a second time in one day. This allows the fish to find a more profitable cell in its new reach.

An evaluation of this approach to outmigration indicates that it produces expected characteristics (Figure 16). When juvenile salmon are small (6 cm and less) they migrate downstream only if growth in their current reach is negative (or if other risks are extremely high). At intermediate lengths (e.g., 8 cm) fish migrate out unless their reach offers low risk and zero to high growth. At lengths approaching 10 cm fish migrate downstream unless their current habitat is extremely safe and offers positive growth. By the length of 12 cm (not shown in Figure 16) all fish have migrated downstream.

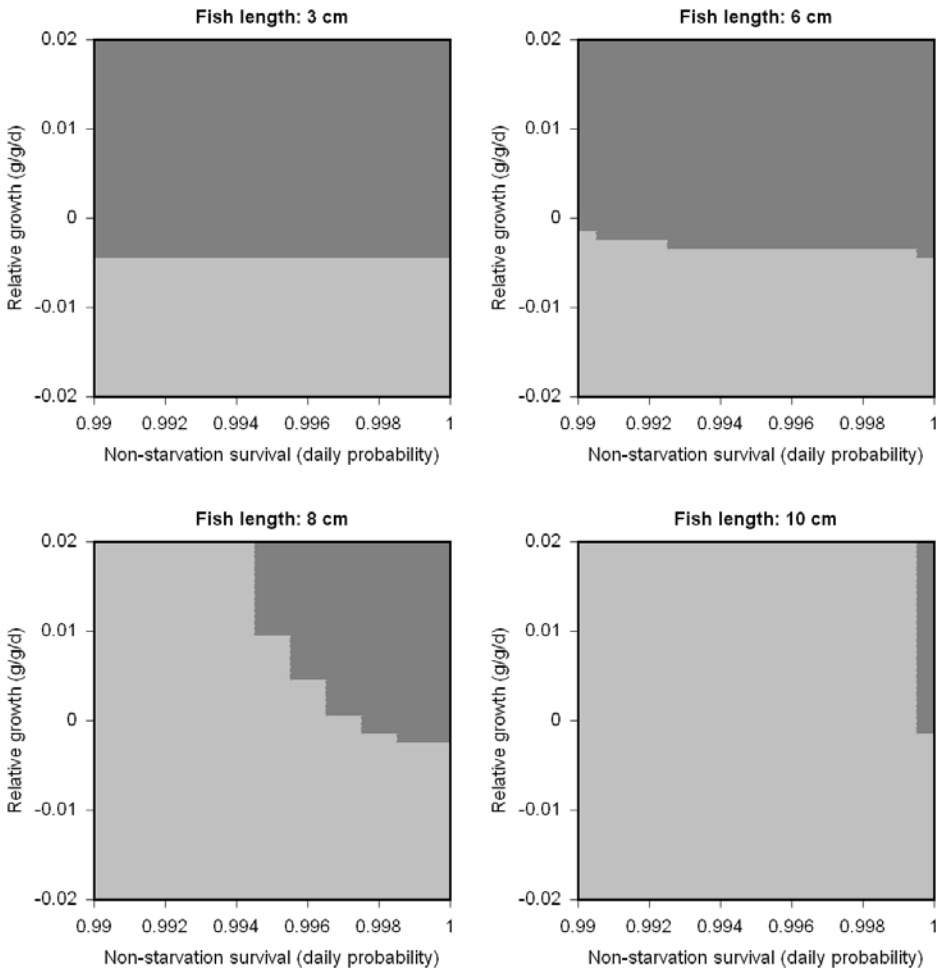

Figure 16. Results of the outmigration decision method with *fishOutmigrateSuccessL1* equal to 5.0 and *fishOutmigrateSuccessL9* at 10.0 cm. Light grey regions indicate combinations of growth and risk conditions under which juvenile salmon migrate downstream, and dark grey regions indicate where salmon remain in the current

reach. The X axis is the daily probability of surviving factors other than starvation (e.g., predation, high temperature). The Y axis is daily growth rate as grams of growth per gram of fish weight. The four panels show how results depend on fish length. Fish were assumed to currently be in good condition; lower condition (weight at length) slightly increases the tendency to migrate downstream.

7.2.6 Removal of outmigrants

Juvenile fish that have migrated downstream beyond the downstream-most reach are treated as "outmigrants". They are removed from the list of live fish and placed on a separate list of outmigrants, and removed from the last habitat cell they occupied. No actions are executed on outmigrants, so they do not change for the rest of the model run. On the day they decide to migrate, outmigrants are not subject to mortality and hence cannot die and outmigrate on the same day.

7.3 Feeding and Growth

7.3.1 Overview

This section describes the methods for determining the daily growth—change in weight and length—that a fish obtain in their habitat cell. These methods are used both in the habitat selection decision to determine how much growth a fish would obtain in each cell it considers as a potential destination, and to simulate growth (the third daily action by fish; Section 11.2). This first subsection provides an overview of the feeding and growth methods, listing the major assumptions. Full detail is provided starting with Section 7.3.2.

Adult salmon follow all the methods for feeding and growth described in this section, but with one major difference: their food intake is always assumed to be zero. Because they still have metabolic costs, adults therefore gradually lose weight. This assumption, combined with the decision of how to feed (Section 7.3.9) and the habitat selection methods (Section 7.2) cause unspawned adults to select feeding behaviors and habitat cells that provide low rates of weight loss and high survival probabilities.

The feeding and growth formulation of *inSALMO* is conceptually related to a number of other models. First, it borrows both basic concepts and detailed methods from the extensive fish bioenergetics literature. The concepts of (1) modeling growth as net energy intake, the difference between energy input from food and energy consumption for metabolism; and (2) modeling metabolic energy consumption as a function of fish size, swimming speed, and temperature; are well-established and tested (to some extent) in the literature (Hanson et al. 1997; see also Brandt and Hartman 1993, Elliott and Hurley 2000). Second, bioenergetics models and feeding models have been combined to predict net energy intake as a function of fish size and habitat conditions (especially, depth and velocity) by a number of researchers (e.g., Fausch 1984, Hughes and Dill 1990, Hill and Grossman 1993, Braaten et al. 1997, Van Winkle et al. 1998, Hayes et al. 2000, Gowan and Fausch 2002, Grossman et al. 2002).

One important characteristic of *inSALMO* is that competition among individual fish for food is modeled. A fish's food intake is assumed to be limited by either the availability of food or the ability of the fish to capture food. The ability to capture food depends on fish size (increasing with length, because larger fish see and swim better) and on habitat conditions such as velocity

and depth in the fish's cell. Food availability depends on how much food is produced in the cell and how much is consumed by competing fish (Section 6.2.6).

Fish in *inSALMO* are assumed to always feed during daylight hours and never at night, a major simplifying assumption. While salmonids have long been thought of as feeding visually and therefore during day, recent literature shows that night feeding is not unusual and under some conditions is more common than daytime feeding (e.g., Fraser and Metcalfe 1997, Metcalfe et al. 1999, Bradford and Higgens 2001). Whether an individual feeds during day or night (or neither) appears to emerge from how mortality risk and food intake vary between day and night, which can in turn vary with fish size, competition, and many habitat variables. How trout choose between feeding during day and night has been simulated successfully in a trout model similar to *inSALMO*, (Railsback et al. 2005), but this capability requires a major increase in the model's complexity. This additional complexity does not appear justified by the objectives of *inSALMO*. While the assumption that salmon feed during daytime only is clearly not always realistic, it is useful for the purposes that *inSALMO* is intended for.

inSALMO does not specify the exact kinds of food consumed by fish, but its feeding formulation and parameters generally represent invertebrate food, not other fish.

Fish in *inSALMO* can use either of two feeding strategies. Drift feeding, in which the fish remains stationary and captures food as it is carried past by the current, is the most studied and often the most profitable strategy (Fausch 1984, Hill and Grossman 1993, Hughes and Dill 1990). Drift food intake is modeled as a function of stream depth and velocity and fish length; intake peaks at an optimal velocity that is higher for larger fish. Drift intake decreases as turbidity increases, as turbidity makes it harder for fish to detect food items. Metabolic costs for drift feeding increase with water velocity, but use of velocity shelters reduces this cost. The second feeding strategy is active searching for food. Search feeding can be important when competition for food is intense, conditions for drift feeding are poor, or the abundance of benthic food is high (Nielsen 1992, Nislow et al. 1998). The energetic benefits of search feeding are assumed to be mainly a function of food availability, with energetic cost depending on water velocity.

The feeding and growth methods calculate the potential food intake and metabolic costs a fish would experience in a cell, for both drift and search feeding. Standard bioenergetics approaches (Hanson et al. 1997) are used by *inSALMO* to calculate net energy intake (the difference between energy intake from food and metabolic energy costs; net energy is often negative) for each feeding strategy. The fish then selects the strategy that provides the highest net energy intake. Growth (increase in body weight, g/d) is proportional to net energy intake.

From a fish's daily growth, its length and condition factor are updated. How an organism allocates its energy intake to growth (increase in length), storage (increase in weight or fat reserves but not length), or gonads is in reality a complex, adaptive decision. For example, a juvenile fish may reduce its risk of predation most by increasing in length as rapidly as possible, but allocating all energy intake to growth instead of storage increases the risk of starvation during periods of reduced intake. However, *inSALMO* does not model energy allocation as an adaptive trait. Instead it uses the approach of Van Winkle et al. (1996) that simply forces fish to maintain a standard relation between length and weight during periods of positive growth.

The method for calculating daily change in length adopted from Van Winkle et al. (1996) also uses their nonstandard definition of a condition factor. In fisheries science, a condition factor is a unitless index of a fish's weight relative to its length. A higher condition factor indicates that a fish is heavy for its length and has high energy reserves, and therefore less vulnerable to starvation or disease during periods of negative growth. The condition factor variable used in *inSALMO* (*fishCondition*) can be considered the fraction of "healthy" weight a fish is, given its length. The value of *fishCondition* is 1.0 when a fish has a "healthy" weight for its length, according to a length-weight relation input to the model via fish parameters *fishWeightParamA* and *fishWeightParamB*:

$$fishHealthyWeight = fishWeightParamA \times fishLength^{fishWeightParamB}.$$

Fish grow in length whenever they gain weight while their value of *fishCondition* is 1.0. Condition factors less than 1.0 indicate that the fish has lost weight. In this formulation, values of *fishCondition* cannot be greater than 1.0. Weight (*fishWeight*, g), length (*fishLength*, cm), and *fishCondition* are calculated in this way.

- The fish's new weight is determined by adding its daily growth (which can be negative) to its previous weight.
- The fish's new weight is used, with the inverted length-weight relation for healthy fish, to calculate *fishWannabeLength*, the length the fish would be if its condition factor were 1.0:

$$fishWannabeLength = \left(\frac{fishWeight}{fishWeightParamA} \right)^{1/fishWeightParamB}.$$

- If the fish's current length is less than *fishWannabeLength* (indicating that the fish is not underweight), then its new length is set to *fishWannabeLength*. The fish grows in length while keeping its *fishCondition* value equal to 1.0.
- If the fish's current length is greater than *fishWannabeLength* (indicating that the fish is underweight for its length), its length is not changed.
- The new value of *fishCondition* is equal to the fish's new weight divided by the "healthy" weight for a fish its length:

$$fishCondition = fishWeight \Big/ \left(fishWeightParamA \times fishLength^{fishWeightParamB} \right).$$

This formulation is simple and succeeds in producing reasonably realistic patterns of growth under many conditions. However, the formulation has several noteworthy limitations:

- Fish cannot store a high-energy-reserve condition. Fish will have a condition of 1.0 *only* on those days when daily growth is positive. Even if a fish has eaten well for many days in succession, its *fishCondition* can only be as high as 1.0 and one day of negative net energy intake causes condition to fall below 1.0. This could be important under

conditions of highly variable food intake because survival is assumed to decrease with condition (Section 7.4.4).

- This weight-based condition factor is not the best predictor of starvation mortality (Section 7.4.4).
- This formulation locks in a length-weight relationship for growing fish. Calibration of growth to situations where this relationship is valid will be automatic, but calibration to situations where the relationship is not valid will be impossible. For example, *inSALMO* cannot predict the existence of unusually fat fish.

These limitations could be eliminated only by making *inSALMO* considerably more complex. Methods for representing energy allocation more realistically in IBMs have not yet been developed and tested. The current formulation appears adequate and appropriate for *inSALMO*'s objectives.

Example parameter values for the length-weight relationship are provided in Table 7. These parameters should not simply be regression parameters calculated from observed data; they must describe a site-specific length-weight relation for fish in good condition.

Table 7. Example parameter values for the length-weight relation, for length in cm and weight in g.

Species and site	Parameter	Value
Juvenile Chinook salmon, Sacramento River (Petrusso and Hayes 2001)	*fishWeightParamA*	0.00411
	fishWeightParamB	3.49

7.3.2 Activity budget

Energy intake and costs differ between feeding vs. resting fish. Energetic calculations are based on hourly energy rates (j/h), and the daily energy totals depend on how many hours are spent feeding vs. resting.

In *inSALMO*, salmon are assumed to spend all daylight hours feeding and all night hours resting. Daylight hours are assumed to include one hour before sunrise and one hour after sunset. Consequently, the time spent feeding per day (*feedTime*, h/d) is *daylength* + 2.

7.3.3 Food intake: drift feeding strategy

Drift feeding fish wait and capture invertebrates as they are carried within range by the current. The drift feeding energy intake formulation of *inSALMO* is unique but conceptually related to the previous feeding and net energy intake models cited in Section 7.3.1. This literature shows clearly that the distance over which fish can see and capture food increases with salmon size and decreases with water velocity. Unlike previous models, *inSALMO* includes the negative effect of turbidity on the ability of salmon to see and capture prey. Turbidity can vary dramatically among sites and over time, and its effects on salmon feeding are strong and relatively predictable. Unlike some previous models of drift feeding, *inSALMO* neglects prey size as a variable. Prey

size is naturally variable and unpredictable, and its effects could not be easily be distinguished from those of other factors.

Drift-feeding fish are assumed to capture some of the food items that pass within a "capture area" (*captureArea*, cm^2), a rectangular area perpendicular to the current, the dimensions of which depend only on fish size (explained below). The fraction of food items passing through the capture area that are actually caught (*captureSuccess*, unitless) decreases with cell velocity, increases with fish swimming ability, and decreases with turbidity. A fish's intake rate (*driftIntake*, g/h) is calculated as the mass of prey passing through the capture area times the capture success:

$$driftIntake = captureSuccess \times habDriftConc \times velocity \times captureArea \times 3600.$$

In this equation, *habDriftConc* (g/cm^3) is a habitat reach variable (Section 6.1.1) and the last term (3600 s/h) converts the rate from per second to per hour.

A detection distance approach is used to calculate *captureArea*. Detection distance is defined as the distance over which fish can see and attack—but not necessarily capture—prey. Detection distance is believed to depend primarily on the size of the fish (bigger fish have bigger, more sensitive eyes) and the size of the prey (bigger prey being easier to detect). Schmidt and O'Brien (1982) collected empirical data on how detection distance in a stream salmonid (arctic grayling) varied with fish and prey size. These experiments used zooplankton as prey, but their results have been used successfully as the basis of drift feeding models of Hughes (1992a) and Hughes et al. (2003). Schmidt and O'Brien (1982) measured detection distance of fish with lengths from 3 to 13 cm, during daylight and night conditions, and for a variety of zooplankton prey sizes. Only daylight observations for 0.2 cm prey (the largest) are used here.

These observations can be represented with a linear model having a slope of 2.0 and intercept of 4.0 cm (Figure 17). This linear model is not a regression fit to the data of Schmidt and O'Brien (1982), and in fact a logarithmic equation fits the data more closely than a line does. The linear model shown in Figure 17 was chosen for several reasons. First, it captures the fact that very small salmon cannot use as wide a range of prey sizes as larger fish can, a process not otherwise represented in the feeding model. Second, a logarithmic fit to these data predicts negative detection distances for salmon lengths less than 2 cm and does not reproduce the observations of Hughes et al. (2003) that detection distance continues to increase to over 100 cm for very large trout. Finally, pre-calibration of the growth model was used to select the intercept and slope of the linear model (parameters *fishDetectDistanceParamA* and *fishDetectDistanceParamB*, defined below). The pre-calibration analysis indicated that the growth rates of very small salmon are very sensitive to the intercept. An intercept of 4.0 was found to provide growth of very small salmon that was realistic at the same drift food availability values that produce realistic growth rates in larger fish.

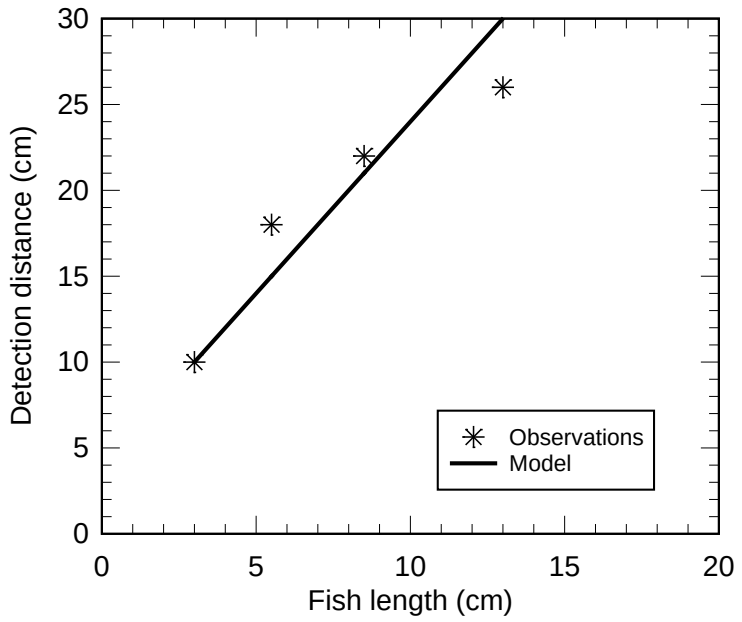

Figure 17. Relation between fish length and prey detection distance observed by Schmidt and O'Brien (1982), for arctic grayling feeding on 0.2 cm zooplankton.

Detection distance is adjusted for turbidity. The primary effect of turbidity on drift feeding appears to be reducing the ability of fish to detect prey: Sweka and Hartman (2001) observed that as turbidity increased the frequency of prey detection by trout decreased, but the frequency of attacking and capturing detected prey did not decrease. Barrett et al. (1992) attempted to evaluate the effect of turbidity on the ability of trout to detect and capture drift food, but their experiment had several weaknesses. The experiment used shallow depths and prey that floated on the surface, likely increasing the fish's ability to detect prey. More importantly, fish and prey were confined to a relatively narrow channel, limiting the ability to measure effects of low turbidity levels because detection distance could exceed the channel width. Sweka and Hartman (2001) conducted a similar experiment but with fewer limitations due to the experimental apparatus. This experiment included a fairly clear test of the effects of turbidity on the ability of fish to detect prey, over a range of 3-40 NTUs. Sweka and Hartman (2001) developed a curve for how detection distance decreases with turbidity, for 14 cm brook trout feeding on large (1.0 cm), floating prey. The function used by *inSALMO* for relative detection distance (the fractional reduction in detection distance due to turbidity, at turbidity levels above zero) is based on the data of Sweka and Hartman (2001) but differs from their curve in two ways.

First, *inSALMO* assumes that turbidity has no effect at values below a threshold of 5 NTUs (defined by the parameter *fishTurbidThreshold*). The curve of Sweka and Hartman (2001) has a steep gradient at low turbidity levels, which would make feeding success very sensitive to low turbidity values. However, none of the literature cited above clearly shows an effect of turbidity at levels below 5 NTUs (see, e.g., Figure 18), and it seems likely that below such a threshold reactive distance is limited by other factors such as turbulence and the ability (or net benefit) of catching food items very far away. Another reason for assuming a turbidity threshold is to avoid making *inSALMO* highly sensitive to low turbidity levels, which are hard to measure or estimate accurately.

The second change is adding a minimum detection distance. The data of Sweka and Hartman (2001) indicate that detection distance does not go completely to zero as turbidity reaches levels well above 50 NTUs. This conclusion is also supported by unpublished studies at Humboldt State University (S. Hadden, unpublished data) which show trout confined to narrow channels able to capture some drift at turbidity levels exceeding 70 NTUs. Therefore, *inSALMO* includes a parameter *fishTurbidMin* which limits the effect of turbidity on detection distance (Figure 18).

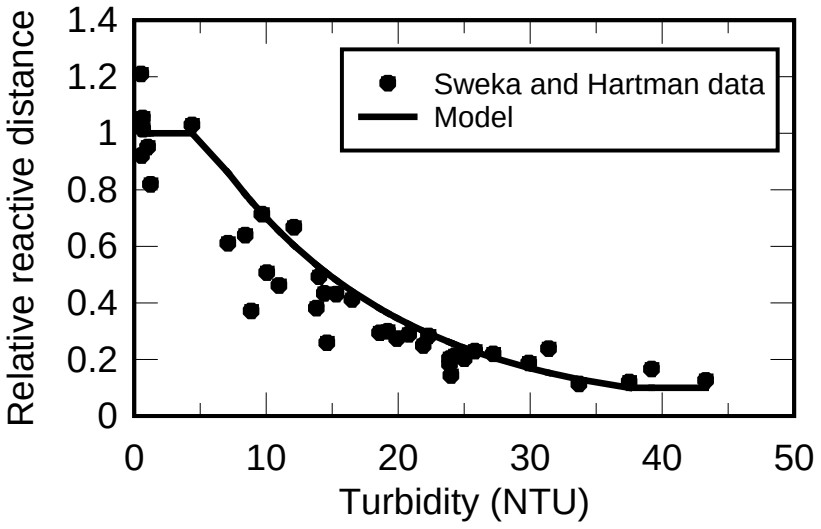

Figure 18. Relative detection distance vs. turbidity: model and data of Sweka and Hartman (2001) used to fit the model.

Detection distance is therefore modeled with this equation:

$$detectDistance = \left[fishDetectDistParamA + \left(fishDetectDistParamB \times fishLength \right) \right] \times turbidityFunction$$

where:

turbidityFunction = 1.0 if *habTurbidity* <= *fishTurbidThreshold*

else *turbidityFunction* =

$$\max\left[\exp\left(fishTurbidExp \times \left(habTurbidity - fishTurbidThreshold \right) \right), fishTurbidMin \right].$$

Parameter values are in Table 8 and the resulting model in Figure 18. The value of *fishTurbidExp* was fit via regression to the data of Sweka and Hartman (2001), who measured absolute reactive distance vs. turbidity by: (1) Establishing the reactive distance for negligible turbidity as the mean of reactive distances observed at turbidities less than 5 NTU; the seven such observations had a mean reactive distance of 80.8 cm. (2) Calculating the relative reactive distance for other observations as the observed reactive distance divided by 80.8. (3) Using exponential regression on relative reactive distance vs. (turbidity - 5 NTU); the regression line was forced through the point (0,1) so relative reactive distance is one when turbidity is 5.

Several previous salmonid feeding models assumed that the capture area is a circle or half-circle with radius equal to the detection distance, but Booker et al. (2004) show that failing to consider depth (which often is less than the detection distance) can cause major errors. *inSALMO* uses a capture area for drift feeding that depends on the detection distance and cell depth. The width of the rectangular capture area is twice the detection distance: fish are assumed able to detect all drift that comes within the detection distance to their left and right, as they face into the current. The height of the capture area is the minimum of the reactive distance and the depth, as fish are assumed more likely to be near the stream bottom than at mid-depth when feeding:

$$captureArea = [2 \times detectDistance] \times [\min(detectDistance, cellDepth)].$$

While the capture area represents the area over which drift-feeding salmon can detect prey, capture success represents what fraction of detected prey are actually caught. Capture success is largely a function of water velocity. Fish must be able to swim to the prey, capture it, and return to their feeding station. At higher velocities, maneuvering quickly enough to capture prey is more difficult, and swimming longer distances after prey requires more energy (because the fish must swim back upstream to return to their feeding station; Hughes et al. 2003). Capture success is also affected by temperature, as the ability of fish to maneuver and swim rapidly is reduced at low temperatures.

Hill and Grossman (1993) measured capture success for rainbow trout feeding on 0.2 cm prey. The trout had lengths of 6 and 10 cm, and measurements were made at 5 and 15ºC with velocities ranging from 0 to 40 cm/s. Capture success was evaluated as the fraction of prey caught, within the fish's detection distance. Hill and Grossman (1993) approximated the detection distance as 2.5 times the fish's standard length, which is fairly close to the detection distance used in *inSALMO* (Figure 17). Hill and Grossman measured capture success within each of three ranges: the inner 20% of the capture distance, 20-60% of capture distance, and 60-100% of capture distance. To develop parameters for *inSALMO*, these values were averaged over the entire capture distance. For all the observations (35 combinations of fish size, temperature, and water velocity), capture success fit a logistic function of the ratio of water velocity to maximum sustainable swimming speed of the fish (Figure 19). (Maximum sustainable swimming speed is a function of fish length and water temperature. The method for modeling it is presented in Section 7.4.2.) Maximum sustainable swim speed (*fishMaxSwimSpeed*) appears to be useful for modeling capture success for two reasons: first, it scales capture success with both fish length and temperature. Second, Hughes et al. (2003) observed that large brown trout actually swim at sustainable (or even lower) speeds when capturing food.

$$captureSuccess = \text{logistic}\left(habVelocity / fishMaxSwimSpeed\right).$$

Parameters for this logistic function are in Table 8.

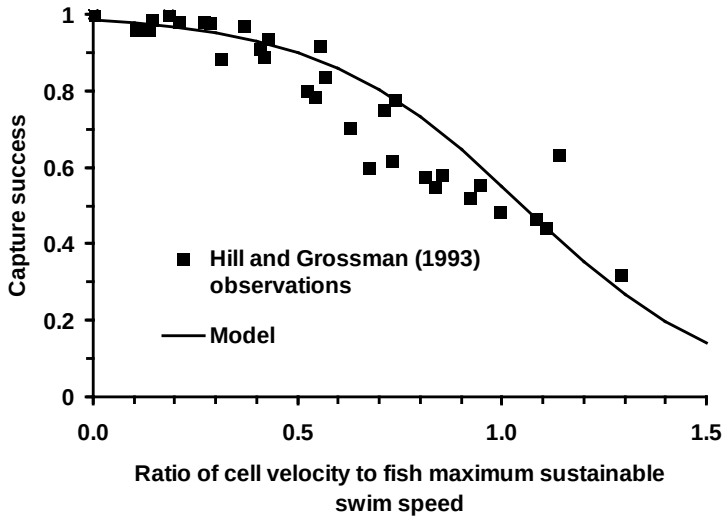

Figure 19. Capture success model and the laboratory observations it was based on.

Table 8. Detection distance and capture success parameters.

Parameter	Definition	Recommended value
fishDetectDistParamA	Intercept in equation for detection distance (cm)	4.0
fishDetectDistParamB	Multiplier in equation for detection distance (unitless)	2.0
fishTurbidThreshold	Highest turbidity that causes no reduction in detection distance (NTU)	5.0
fishTurbidExp	Multiplier in exponential term for the turbidity function (unitless)	-0.0711
fishTurbidMin	Minimum value of the turbidity function (unitless)	0.1
fishCaptureParam1	Ratio of cell velocity to fish's maximum swim speed at which capture success is 0.1 (unitless)	1.6
fishCaptureParam9	Ratio of cell velocity to fish's maximum swim speed at which capture success is 0.9 (unitless)	0.5

7.3.4 Food intake: active searching strategy

Actively searching for benthic or drop-in food is an alternative to the drift-feeding strategy. Unlike drift feeding, there are no established models for search feeding by salmon. An optimal foraging approach would be to assume fish search for food at a rate that maximizes the difference between energy intake from feeding and energy cost of swimming. To avoid the complexity of such an approach, *inSALMO* simply assumes that the rate of search food intake is proportional to the rate at which search food becomes available: every fish searches for food at about the same rate, so intake increases linearly with food production. Search feeding intake is also assumed to decrease linearly to zero as water velocity increases to the fish's maximum sustainable swim speed. This velocity function represents how the ability of a fish to see and search for food decreases with velocity. (It does *not* represent the energetic cost of swimming at high velocities, which is considered in the respiration formulation; Section 7.3.7.) Search food intake is assumed zero for cells of zero depth.[6]

The search food intake model is:

[6] Zero search intake at dry cells is new in *inSALMO* 1.5.

$$searchIntake = habSearchProd \times fishSearchArea \times \max\left(\left[\frac{fishMaxSwimSpeed - cellVelocity}{fishMaxSwimSpeed}\right], 0\right)$$

where *searchIntake* (g/h) is the rate at which food is taken in via search feeding, *habSearchProd* (g wet weight/h-cm^2) is the rate at which search food is produced (Section 6.2.6), *fishMaxSwimSpeed* is the fish's maximum sustainable swimming speed (cm/s; Section 7.4.2), and *cellVelocity* (cm/s) is the velocity of the fish's cell. The proportionality constant *fishSearchArea* (cm^2) can be loosely interpreted as the area over which the production of stationary (non-drifting) food is consumed by one fish. This search area is not necessarily a contiguous piece of stream area: a small fish searching a small area closely may obtain the same food intake as a big fish spot-searching over a much larger area. Because *habSearchProd* and *fishSearchArea* have the same effect on search intake and both would be very difficult to measure, either would be a good parameter to use for calibration. Note that fish size does not affect search food intake except for the effect of size on *fishMaxSwimSpeed*; therefore, search feeding is more likely to be the desirable strategy for smaller fish.

Note that turbidity is not assumed to affect search feeding. While search feeding can sometimes be primarily visual, anecdotal evidence (e.g., observations of trout with full stomachs, foraging along stream margins during extremely turbid flood flows) indicate that salmonids can search-feed successfully using other senses. DeRobertis et al. (2003) conducted tank experiments resembling search feeding by juvenile chum salmon, observing feeding success at various turbidity levels. Feeding success under daytime conditions did not decrease consistently at turbidities between zero and 20 NTU; at 40 NTU feeding success was about one third of that in clear water. (During nighttime light levels, even turbidities up to 40 NTU caused no decrease in feeding success.) Because the effects of turbidity on search feeding are apparently limited, they are ignored in *inSALMO*.

7.3.5 Food intake: maximum consumption

As part of the net energy intake calculations, calculated food intake from drift or search feeding is checked to make sure it does not exceed the physiological maximum daily intake. This maximum daily consumption, referred to as *cMax* (g/d) in the bioenergetics literature, represents the maximum rate of food consumption if a fish is limited only by its physiology. Field bioenergetics studies (Preall and Ringler 1989, Railsback and Rose 1999) indicate that actual food intake does not approach *cMax* under typical conditions. However, here *cMax* serves the purpose of restricting intake and growth during low temperatures, a function otherwise lacking in the model (except that the time spent feeding becomes zero at temperatures below a threshold; Section 7.3.2). Cunjak et al. (1998) cite evidence that low food assimilation efficiencies and gut evacuation rates, which can be represented by *cMax*, limit energy intake in cold temperatures.

Unfortunately, *cMax* is poorly defined and difficult to measure, largely because it varies with factors such as the fish's exercise condition, food type, and feeding conditions in the laboratory (PG&E 1994, Myrick 1998). However, there are a number of published equations for *cMax* that

include (a) an allometric function, relating *cMax* to fish size; and (b) a temperature function (Hanson et al. 1997). The equation used in *inSALMO* is:

$$cMax = fishCmaxParamA \times fishWeight^{(1+fishCmaxParamB)} \times cmaxTempFunction.$$

This equation is widely used with the parameters developed by Rand et al. (1993) for rainbow trout (Table 9) for modeling *cMax* of salmonids in general (e.g., Van Winkle et al. 1996, Railsback and Rose 1999, Booker et al. 2004).

The *cMax* temperature function used in *inSALMO* is based in part on laboratory studies on rainbow trout by Myrick (1998) and Myrick and Cech (2000). These studies focused on higher temperatures, measuring *cMax* at 10, 14, 19, 22, and 25ºC. Previous models of *cMax* for salmonids (Rand et al. 1993) used temperature functions based on the laboratory studies of From and Rasmussen (1984), who studied rainbow trout at temperatures of 5-22ºC; and of Elliott (1982) who studied brown trout. Instead of an equation, the *cMax* temperature function is a set of seven points used to interpolate a value of *cmaxTempFunction* from the temperature of a fish's habitat reach (Table 10).

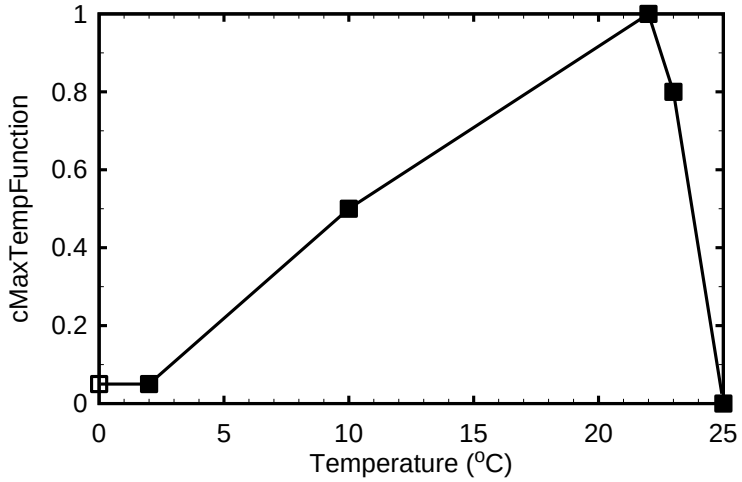

Figure 20. Temperature function for *cMax*.

While several sets of equations and parameters for *cMax* have been published for different salmonid species, careful scrutiny of these publications indicate that the differences in models of *cMax* are more likely to result from differences in experimental methods than from differences among species or stocks. Considering the inherent uncertainty in *cMax* and its limited effect on results of *inSALMO*, the parameters in Table 9 and Table 10 are cautiously recommended for all stream salmonid species.

■

Table 9. Parameter values for allometric function of maximum consumption.

Parameter	Definition	Value
fishCmaxParamA	Allometric constant in *cMax* equation (unitless)	0.628
fishCmaxParamB	Allometric exponent in *cMax* equation (unitless)	-0.3

Table 10. Parameter values for temperature function of maximum consumption. Each row in the table defines one of the points in Figure 20.

Parameter Name	Temperature (°C)	Parameter Name	Temperature Function Value (unitless)
fishCmaxTempT1	0	*fishCmaxTempF1*	0.05
fishCmaxTempT2	2	*fishCmaxTempF2*	0.05
fishCmaxTempT3	10	*fishCmaxTempF3*	0.5
fishCmaxTempT4	22	*fishCmaxTempF4*	1.0
fishCmaxTempT5	23	*fishCmaxTempF5*	0.8
fishCmaxTempT6	25	*fishCmaxTempF6*	0
fishCmaxTempT7	100	*fishCmaxTempF7*	0

7.3.6 Food intake: daily food availability

The food intake of each fish can be limited by the total amount of drift (*driftDailyCellTotal*, g/d) and search (*searchDailyCellTotal*, g/d) food available each day in its cell. These daily food availability values are a function of the fish's feeding time (*feedTime*, h; Section 7.3.2) because food produced during non-feeding hours cannot be considered available to the fish. The daily food availability rates are calculated from the hourly food availability rates described in Section 6.2.6.2. The hourly availability rates are the rate at food is produced in the cell, minus food consumption by larger fish. Therefore, hierarchical competition for food is implemented via the food availability rates. Daily food availability for a fish is determined as:

$$driftDailyCellAvail = driftHourlyCellAvail \times feedTime$$

and:

$$searchDailyCellAvail = searchHourlyCellAvail \times feedTime$$

where *driftHourlyCellAvail* and *searchHourlyCellAvail* are as defined in Section 7.3.2.

7.3.7 Respiration costs and use of velocity shelters

Conventional bioenergetics modeling approaches for fish (Hanson et al. 1997) model respiration as the energetic cost of metabolism and swimming. This approach is adopted for *inSALMO*, modeling (a) standard respiration that is independent of the fish's activity, and (b) an additional activity respiration that increases with the daily swimming speed.

Swim speeds. Drift-feeding fish are assumed to swim at a speed (*swimSpeed*, cm/s) equal to their habitat cell's water velocity unless they have access to velocity shelter. Fish using the search feeding strategy are assumed to swim at a speed equal to their cell's mean water velocity. These two assumptions are a highly simplified representation of how real salmon swim within a day, but the consequent error in respiration costs is neglected instead of making the model more complex.

If a drift-feeding fish has access to velocity shelter, then its *swimSpeed* is assumed equal to a constant fraction of its habitat cell's mean water velocity. This fraction is defined by the habitat parameter *habShelterSpeedFrac*. A number of studies have shown that "focal" water velocities (the velocity measured as closely as possible to the spot where a fish was drift-feeding) are related to, but less than, the depth-averaged velocity at the same location (e.g., Baltz and Moyle 1984, Baltz et al. 1987, Moyle and Baltz 1985). However, relations between focal and depth-averaged velocities observed in these studies are not directly applicable to *inSALMO* because *habShelterSpeedFrac* approximates the difference between cell average water velocity and the swimming speed of a fish using velocity shelter. The best value of this parameter will vary with the kind of velocity shelter being used and could easily be estimated in the field by using a velocity meter. For a small, hydraulically complex stream with velocity shelter due to boulders and logs, Railsback and Harvey (2001) used a value of 0.3 for *habShelterSpeedFrac*. For the Green River, Utah, where substrates are relatively small and embedded, a value of 0.5 was used (Railsback et al. 2005).

Velocity shelter access. Model salmon are assumed to compete for available velocity shelter space, similar to how they compete for available food. The following steps determine whether each fish has access to shelter in a habitat cell.

- Each cell has a limited area of velocity shelter; this area varies among cells but is constant over time (Section 6.2.3).

- Each drift-feeding fish is assumed to use up an area of velocity shelter equal to the square of its length.

- A fish has access to velocity shelter in a cell only if the sum of shelter areas occupied by larger drift-feeding fish in the cell is less than the cell's total shelter area.

Each fish is assumed to use only a small shelter area (the square of its length) to ensure that fish compete with each other for food, not for shelter area, unless velocity shelter clearly limits net energy intake.

Respiration cost model. *inSALMO* uses the Wisconsin Model equation 1 for respiration (Hanson et al. 1997), as modified by Van Winkle et al. (1996) to apply the activity respiration

rate only during active feeding hours. The parameters that Rand et al. (1993) developed for steelhead trout (converted from calories to joules; Table 11) are widely used and appear to be the best available for stream salmonids in general. This formulation breaks respiration into two parts: standard respiration (*respStandard*, j/d) takes place 24 h/d and includes no effect of activity; activity respiration (*respActivity*, j/d) is the energy needed to swim during feeding. Total respiration (*respTotal*, j/d) is the sum of these two. The equations are:

$$respTotal = respStandard + respActivity\,,$$

$$respStandard = \left(fishRespParamA \times fishWeight^{fishRespParamB} \right) \times \exp\left(fishRespParamC \times temperature \right)$$

and

$$respActivity = \left(\frac{feedTime}{24} \right) \times \left[\exp\left(fishRespParamD \times swimSpeed \right) - 1 \right] \times respStandard\,.$$

Data collected by Myrick (1998; see also Myrick and Cech 2000) indicate that the standard respiration formulation overestimates the effect of temperature on respiration rates and does not account for a decrease in respiration observed at temperatures above 22°. Because of the Wisconsin Model equation's exponential temperature function, these problems cannot be fixed by changing parameter values. However, realistic calibrations of growth have been made with this formulation. The decrease in respiration by inactive fish at high temperatures observed by Myrick (1998) in laboratory respiration chambers may not be applicable in natural settings.

Table 11. Parameter values for respiration.

Parameter	Definition	Units	Value
fishRespParamA	Allometric constant in standard respiration equation	*	30
fishRespParamB	Allometric exponent in standard respiration equation	none	0.784
fishRespParamC	Temperature coefficient in standard respiration equation	1/°C	0.0693
fishRespParamD	Velocity coefficient in activity respiration equation	s/cm	0.03

*This is an empirical parameter with units that depend on *fishRespParamB*.

7.3.8 Other energy losses

Many fish bioenergetic formulations include terms for energy losses due to egestion, excretion, and specific dynamic action. These terms are not included in *inSALMO* because their effects are

small compared to the uncertainties and variability in food availability and in the feeding and growth formulation (Bartell et al. 1986). These terms may be important at extremely low or high temperatures when the ability to digest food can limit growth; instead, *inSALMO* uses the *cMax* function to limit food consumption at extreme temperatures.

7.3.9 Feeding strategy selection, net energy benefits, and growth

The feeding strategy selection, net energy, and growth methods calculate a fish's daily growth for a specific habitat cell. Total food and energy intake is calculated and total energy losses subtracted, determining whether drift feeding or active searching is more profitable.

Variables with the word "food" in their name refer to prey, in g; "energy" variables refer to energy from prey (j). Prey energy density (the habitat parameter *habPreyEnergyDensity*, j/g) is used to convert grams of prey eaten to joules of energy intake. Values of *habPreyEnergyDensity* are provided for various prey types by Hanson et al. (1997). A value of 2500 j/g is reasonable for streams where drift prey is dominated by aquatic insect larvae; a value of 4000 j/g is appropriate for streams where drift is dominated by higher-energy prey such as amphipods. Parameter *habPreyEnergyDensity* applies to both drift and search food.

The energy density of fish (fish parameter *fishEnergyDensity*, j/g) is used to convert a fish's net energy intake to growth in weight. The energy density of salmonids actually varies through their life cycle (typically higher in adults, especially during gonad development prior to spawning), but this variation is ignored in *inSALMO*. The literature summarized by Hanson et al. (1997) indicates that 5900 j/g is a reasonable value for all stream salmonids.

The following steps describe the process used by a fish to determine the feeding strategy it would use, and the resulting food intake and growth it would obtain, for a particular habitat cell. This process uses variables (e.g., *driftIntake*, *feedTime*, *searchIntake*) calculated using the methods described above.

1. Determine the daily drift intake that would be obtained in the absence of more dominant fish in the cell. This *dailyPotentialDriftFood* (g/d) is determined from the hourly intake rates and hours spent feeding:

   $$dailyPotentialDriftFood = driftIntake \times feedTime.$$

2. Determine *dailyAvailableDriftFood*, the drift intake rate available after more dominant fish in the cell have consumed their intake.

3. Calculate the actual drift intake rate *dailyDriftFoodIntake* (g/d), considering whether it is limited by actual food availability or the physiological maximum intake, *cMax*:

   $$dailyDriftFoodIntake = \min(dailyPotentialDriftFood, dailyAvailableDriftFood, cMax).$$

4. Convert daily drift intake in grams of food to joules of energy, *dailyDriftEnergyIntake* (j/d):

   $$dailyDriftEnergyIntake = dailyDriftFoodIntake \times habPreyEnergyDensity.$$

5. Conduct the bioenergetics energy balance to get net energy intake for drift feeding; total respiration (*respTotal*, j/d) depends on cell velocity and whether the fish has access to velocity shelter:

   dailyDriftNetEnergy = dailyDriftEnergyIntake - respTotal.

6. Determine the daily search feeding intake that would be obtained in the absence of more dominant fish in the cell, *dailyPotentialSearchFood* (g/d):

   dailyPotentialSearchFood = searchIntake × *feedTime*.

7. Determine *dailyAvailableSearchFood*, the search intake is available after more dominant fish have consumed their intake.

8. Calculate the actual search intake *dailySearchFoodIntake* (g/d), considering whether it is limited by food availability or maximum daily intake:

   dailySearchFoodIntake = min(*dailyPotentialSearchFood, dailyAvailableSearchFood, cMax*).

9. Convert daily search intake to joules of energy, *dailySearchEnergyIntake* (j/d):

   dailySearchEnergyIntake = dailySearchFoodIntake × *habPreyEnergyDensity*.

10. Conduct the bioenergetics energy balance to get net energy intake for search feeding:

    dailySearchNetEnergy = dailySearchEnergyIntake - respTotal.

11. Select the most profitable feeding strategy by comparing *dailyDriftNetEnergy* to *dailySearchNetEnergy*; and determine the energy intake for the best strategy:

    bestNetEnergy = max(*dailyDriftNetEnergy, dailySearchNetEnergy*).

12. Convert net energy intake to daily growth dailyGrowth (g/d):

    dailyGrowth = bestNetEnergy / fishEnergyDensity.

13. Update the fish's weight:

    fishWeight = fishWeight + dailyGrowth.

In the final step, *fishWeight* is not allowed to become negative; it is set to zero if *dailyGrowth* is negative with a magnitude greater than *fishWeight* (this can happen in the model, although biologically unrealistic, when small fish calculate growth for cells where swimming speed would be extremely high).

Examining how food intake and growth vary with cell velocity helps understand the feeding and growth formulation. Figure 21 illustrates how daily food intake (evaluated as the percent of

cMax) varies with velocity, for both 5 cm juveniles and 15 cm salmonids, for both feeding strategies. Figure 22 illustrates the resulting growth (as percent body weight per day), also showing the effect of using velocity shelters on growth. These graphs assume the temperature is 15°, depth is 50 cm, feeding time is 16 h/d, *habShelterSpeedFrac* is 0.3, *habDriftConc* is 5×10^{-10}, and *habSearchProd* is 5×10^{-7} g/cm^2/h. Figure 23 is identical to Figure 22 except for depicting winter conditions, with a temperature of 5ºC and feeding time of 12 h.

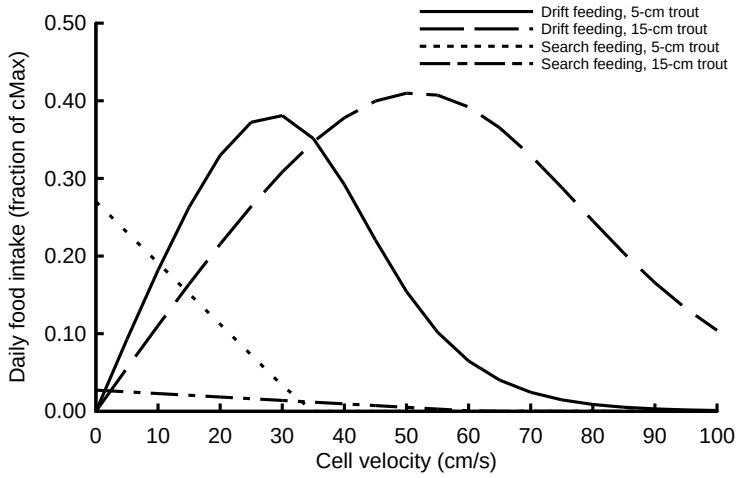

Figure 21. Variation in food intake with velocity for two sizes of salmonid, using drift or search feeding. Intake is depicted as percent of *cMax* (physiological maximum daily intake).

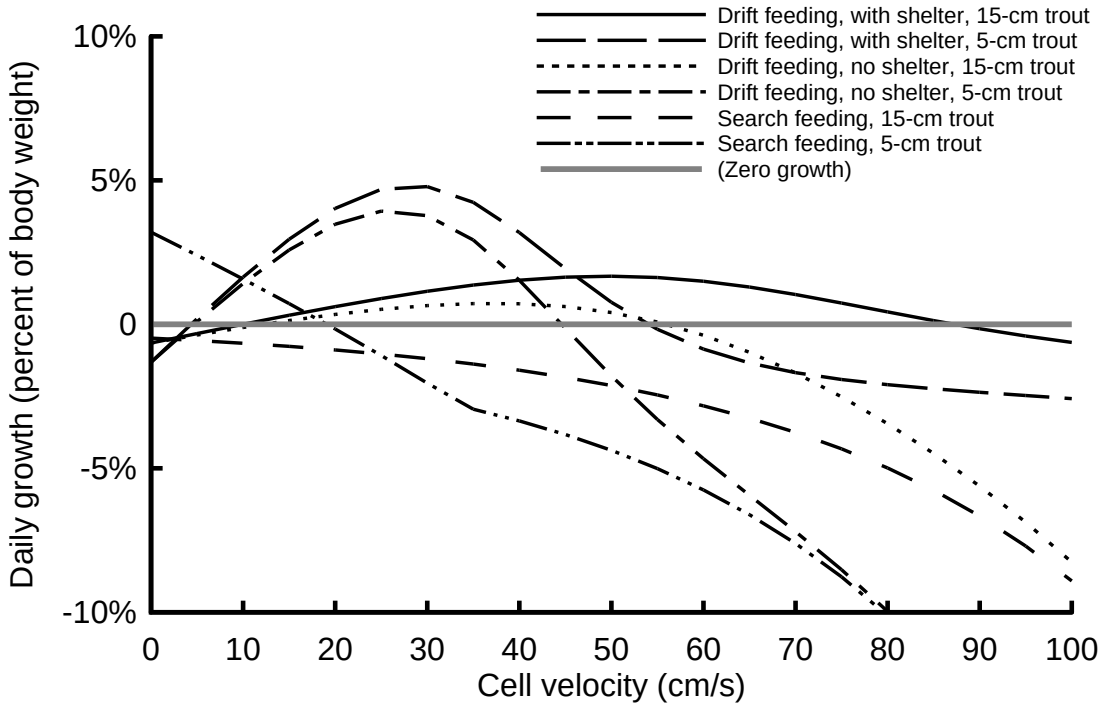

Figure 22. Variation in growth rate with velocity for two sizes of salmonid, drift and search feeding strategies. Growth is depicted as percent of body mass per day.

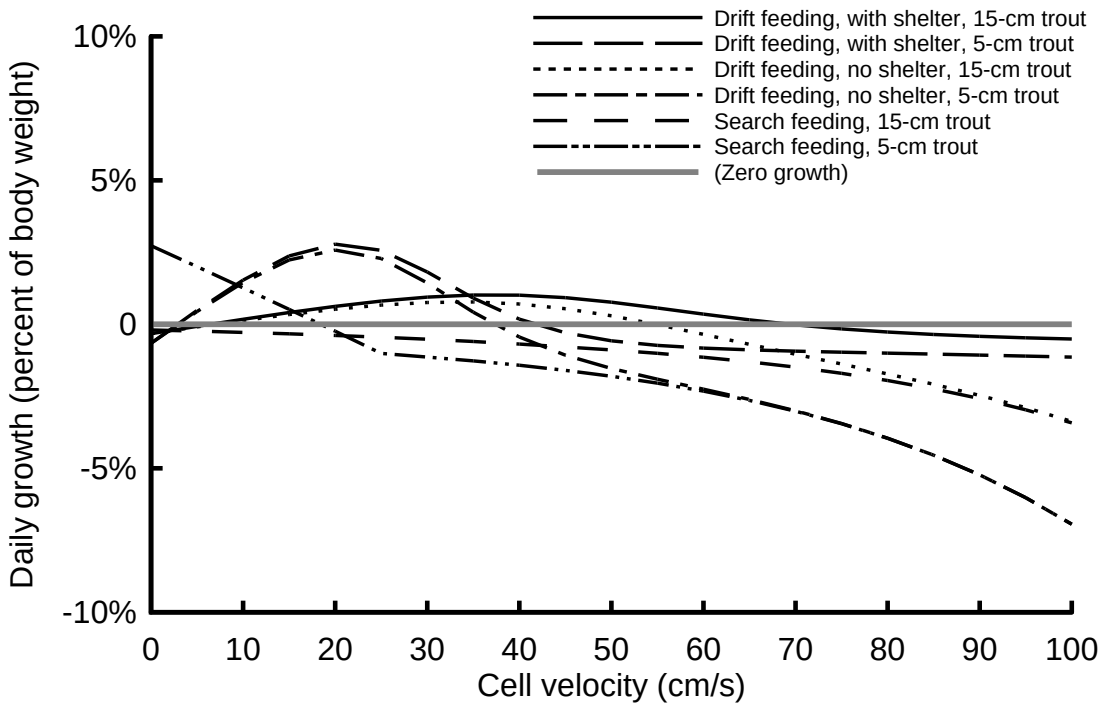

Figure 23. Variation in growth rate with velocity, under winter conditions.

Several patterns in these results are noteworthy in that they appear to reflect patterns observed in real salmon:

- Conditions providing high intake do not always provide high growth, due to the metabolic costs of swimming (especially for fish drift feeding without velocity shelters).
- The use of velocity shelters for drift feeding is very beneficial. Shelters increase the growth rate but also, more importantly, increase the range of velocities under which growth is positive.
- Larger fish can drift feed profitably over a wider range of velocities, and at higher velocities, than can smaller fish.
- Search feeding is a profitable strategy only for small fish in low velocities.
- The relative benefits of drift feeding increase with fish size.
- When temperatures are lower, growth is lower and optimized at lower velocities.

7.4 Fish Survival

Survival simulations determine, each day, which fish die from what causes. The survival action for a fish is a two-step process. First is calculating the probability of surviving each of several mortality sources. Second is determining, stochastically, whether the fish actually dies due to any of the mortality sources.

The survival methods simulate important mortality sources: environmental and biological processes that can kill fish. Mortality sources are represented in *inSALMO* as survival

probabilities: the daily probability of not being killed by one specific mortality source. The mortality sources in *inSALMO* are:

- High temperature,
- High velocity (exhaustion and inability to maintain position),
- Stranding (including predation risk associated with extremely shallow habitat),
- Poor condition (starvation and disease when weight is low),
- Predation by terrestrial animals, and
- Predation by fish.

The primary reason that *inSALMO* represents these different mortality sources separately is that the probability of surviving each varies differently with fish state and habitat conditions. For example, the risk of predation by terrestrial animals is greatest for large fish in shallow, low-velocity cells; the risk of predation by fish is greatest for small fish in deep cells. The primary adaptive behavior represented in *inSALMO*—habitat selection—depends on survival probabilities. For habitat selection to be modeled realistically, *inSALMO* must represent how different mortality sources vary differently over time, among fish, and over space. High temperature is included as a mortality source not as much because it affects habitat selection as because it is a way that river management can directly affect salmon.

Survival probabilities are used for two purposes. First, survival probabilities are used during habitat selection (Section 7.2) as a major input fish use in deciding which habitat cell to occupy. The second use, addressed here, is to model mortality: when and why each fish actually dies. The same methods are used to determine survival probabilities in modeling both habitat selection and mortality.

Death of fish is modeled stochastically by comparing pseudo-random numbers to the survival probabilities. Potential death due to each mortality source is treated as an independent event. On each simulated day, each fish determines whether it dies of each mortality source using these steps:

- Calculate the survival probability from the current state of the fish and its cell.
- Obtain a pseudo-random number from a uniform distribution between zero and one.
- If the random number is greater than the survival probability, then the fish dies as a result of the mortality source. No further mortality sources are evaluated for the fish.
- If the fish does not die, then the next mortality source is evaluated.

While death due to each mortality source is treated independently, the order in which mortality sources are evaluated can have a (usually very small) effect on how many fish die of each kind of mortality. The ordering of mortality sources is discussed with the model schedule in Section 11.2.

It is important to understand that seemingly high daily survival probabilities can result in low survival over time. For example, a daily survival probability of 0.99 results in mortality of 26 percent of fish within 30 days ($0.99^{30} = 0.74$). Survival probabilities should be well above 0.99 if they are not to cause substantial mortality over time. It is often helpful to translate daily survival values into the probability of surviving for 30 days and think about monthly survival.

The following sections describe the detailed formulation used to calculate survival probabilities for each mortality source.

7.4.1 High temperature

This mortality source represents the breakdown of physiological processes at high temperatures. It does not represent the effect of high temperatures on bioenergetics (reduced growth at high temperature). The high temperature survival function is based on laboratory data collected from (presumably) disease-free fish, so it does not represent the effect of disease even though fish are probably more susceptible to disease at high temperatures. Instead, disease is modeled as part of poor condition mortality; a fish able to maintain its weight at sublethal temperatures is assumed to remain healthy.

While input to *inSALMO* includes only daily mean temperature, mortality is related to the daily maximum temperature as well as the mean (although the relative importance of mean v. maximum temperature is not clear: Dickerson and Vinyard 1999, Hokanson et al. 1977). The survival probability parameters therefore assume a difference between mean and peak temperatures. The temperature mortality parameters can be re-evaluated for sites with particularly high or low diurnal temperature variations.

High temperature mortality has been addressed by numerous laboratory studies, but models of this mortality remain variable and uncertain because mortality varies with laboratory conditions and techniques and the endpoints used to define mortality; varies between laboratory and field conditions; and undoubtedly varies among individuals. Review of such literature compilations as Behnke (1992) and Moyle and Marchetti (unpublished) indicates that any differences in measured lethal temperatures among salmonid species are not clearly distinguishable from uncertainty and variability in the measurements. Recent laboratory data showed approximately 60 percent survival of golden trout (*Oncorhynchus mykiss*) juveniles over a 30-d period at a constant 24° (Myrick 1998), equivalent to a daily survival of 0.98. Dickerson and Vinyard (1999) measured survival of Lahontan cutthroat trout (*O. clarki*) for 7 d at high temperatures, finding zero survival at 28°, 40 percent survival at 26° (equivalent to daily survival of 0.88), and 100 percent survival at 24°. This literature indicates that high temperature mortality can be modeled well as a logistic function. The parameters in Table 12 (illustrated in Figure 24) were derived from information compiled by Myrick and Cech (2004); they produce survival survival of 0.98 at 24°, 0.88 at 26°, and < 0.5 at 28°.

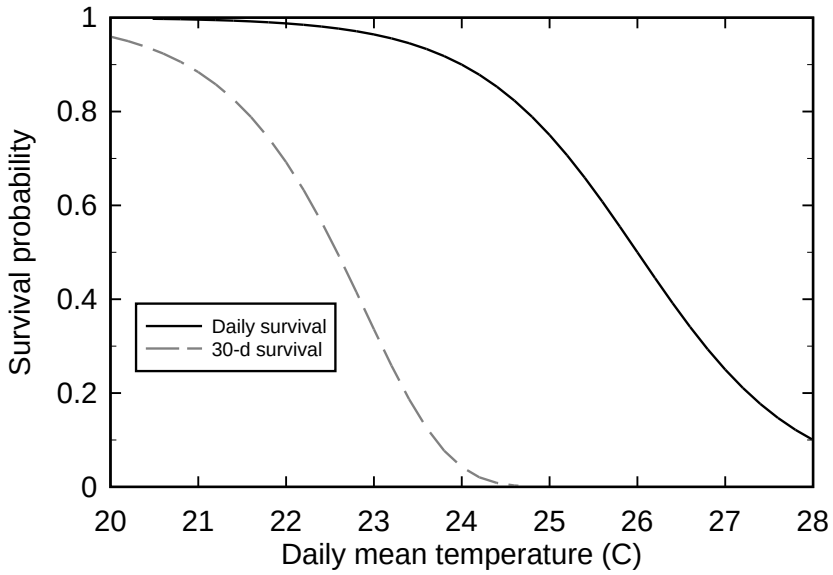

Figure 24. Survival probability function for high temperature. Daily survival (solid line) is the probability of a salmon surviving high temperature mortality for one day. 30-d survival (dashed line) is the probability for surviving the temperature for 30 days (equal to the daily survival raised to the power 30).

Table 12. Parameter values for high temperature mortality.

Parameter	Definition	Value
mortFishHiTT9	Daily mean temperature (°C) at which high temperature survival is 90 pct	24
mortFishHiTT1	Daily mean temperature (°C) at which high temperature survival is 10 pct	28

7.4.2 High velocity

The high velocity survival function represents the potential for salmon to suffer fatigue or lose their ability to hold position in a cell with high velocity. This function is included not because salmon often die due to high velocity, but because it strongly affects habitat selection: mortality due to high velocities is not observed in nature because fish avoid it by moving. Velocities posing mortality risk can be widespread at high flows, but can also occur (especially for small fish) at normal flows.

The survival probability is based on the ratio of the swimming speed a fish uses in a cell to the fish's maximum sustainable swim speed. The swimming speed used in a cell is determined when calculating respiration energy costs (Section 7.3.7): fish are assumed to swim at the cell's water velocity unless they are drift-feeding with access to velocity shelters. Fish using velocity shelters

are assumed to swim at a speed equal to the cell's velocity times the parameter *habShelterSpeedFrac*.

Maximum sustainable swim speed (*maxSwimSpeed*, cm/s) is a particularly important state variable for model salmon. As a component of both high velocity mortality and drift feeding (Section 7.3.3), *maxSwimSpeed* strongly affects the relationship between a cell's velocity and habitat quality for various size salmon. Because *inSALMO* uses a daily time step, the maximum swim speed used for high velocity mortality must be a speed that fish can swim for hours, not a burst or short-term maximum speed. The formulation for *maxSwimSpeed* is based on literature values of "critical swimming speed" (often abbreviated as U_{crit}), a standard approach to estimating maximum sustainable speed in a laboratory test chamber. Measurement of U_{crit} involves repeatedly stepping up the swimming speed and holding it for a specified time interval until the fish is exhausted; different time intervals can be used to estimate short-term vs. long-term sustainable swim speeds. To model *maxSwimSpeed*, long-term values of U_{crit} were used. Myrick (1998) cites references indicating that salmonids may start to use white (fast-twitch) muscle fibers at 90-95 percent of U_{crit}. Therefore, a better estimate of the speed fish can sustain for long periods is 90 percent of the U_{crit} (C. Myrick, Department of Fish, Wildlife, and Conservation Ecology, University of California, Davis, pers. comm. with S. Railsback, 10 May 1999).

U_{crit} for stream salmonids has been measured at different temperatures and fish lengths by a number of researchers. These studies examined brown (Butler et al. 1992), cutthroat (Hawkins and Quinn 1996, MacNutt et al. 2004), and rainbow and golden trout (Schneider and Connors 1982; Taylor et al. 1996; Alsop and Wood 1997; Myrick 1998, also published in Myrick and Cech 2000; Myrick and Cech 2003). [The study by Griffiths and Alderdice (1972) was not used even though it has been the basis of several previous models of maximum swimming speed. Griffiths and Alderdice measured juvenile coho salmon swimming speed over temperatures between 2 and 26° C; however, they did not provide sufficient information to distinguish the effects of fish size and temperature and apparently did not control these two variables separately.]

There is considerable variability among these studies, likely due to differences in experimental equipment and techniques, and to variability in the exercise condition of the fish. However, two general conclusions can be drawn. First, *maxSwimSpeed* increases with fish length (Figure 25). Second, *maxSwimSpeed* varies nonlinearly with temperature, peaking at temperatures around 10-15º (Figure 26). The formulation for *maxSwimSpeed* therefore has two terms: the first represents how swimming speed at 10-15º varies with fish length, and the second modifies *maxSwimSpeed* for temperature.

$$maxSwimSpeed = [(fishMaxSwimParamA \times fishLength) + fishMaxSwimParamB] \times [(fishMaxSwimParamC \times temperature^2) + (fishMaxSwimParamD \times temperature) + fishMaxSwimParamE]$$

Parameter values are in Table 13. These parameters were fit to data from the studies cited above. Observations of U_{crit} from these studies were converted to maximum sustainable swimming speeds by multiplying U_{crit} by 0.9. The relation between *maxSwimSpeed* and salmon length (parameters *fishMaxSwimParamA* and *fishMaxSwimParamB*) was fit using observations made at

temperatures between 10 and 15ºC (Figure 25). A few of these literature values were omitted as outliers (as shown in the figures) because they appeared to underestimate swim speed. Parameters *fishMaxSwimParamC*, *fishMaxSwimParamD*, and *fishMaxSwimParamF* were fit via polynomial regression of (a) the ratio of swim speed at a temperature to swim speed at 15º in the same study, vs. (b) temperature (Figure 26).

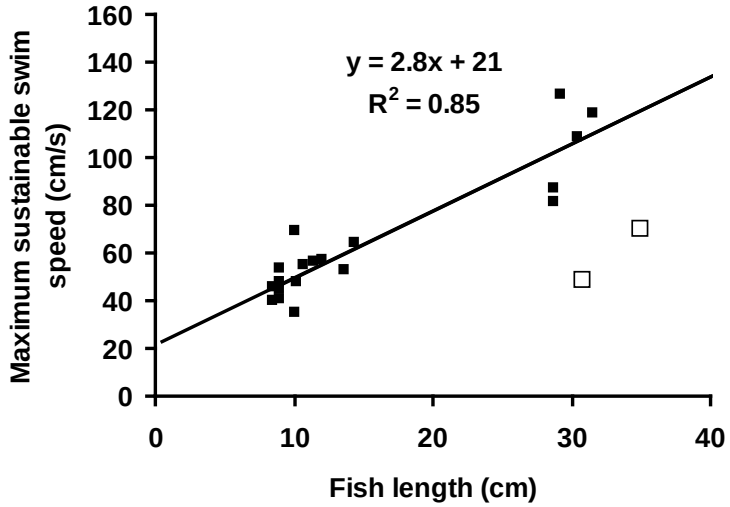

Figure 25. Maximum sustainable swimming speed as a function of fish length; measurements made at 10-15º C. The points marked as open squares were omitted as outliers.

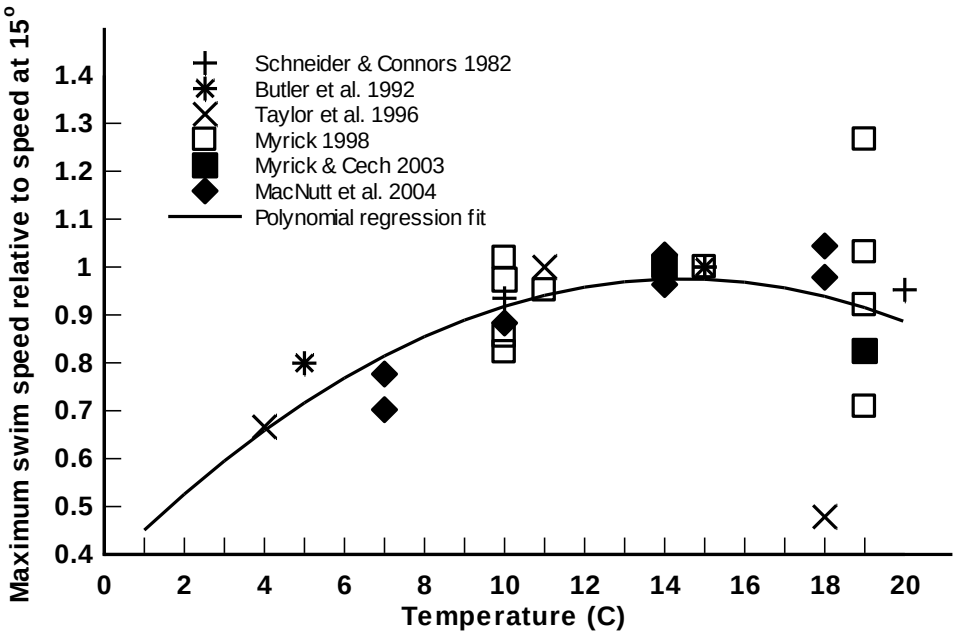

Figure 26. Variation in maximum sustainable swim speed with temperature. Observations from four studies are shown separately. The Y axis is the measured swim speed divided by the speed measured at (or near) 15° in the same study.

A decreasing logistic function relates survival probability to the fish's swimming speed in its habitat cell divided by the fish's value of *maxSwimSpeed* (Figure 27). The parameters for this function (Table 13) are chosen so that high velocity mortality is negligible at swimming speeds less than *maxSwimSpeed*, reflecting that (a) the laboratory equipment for measuring swim speeds does not provide the kinds of turbulence and fine-scale velocity breaks that salmon can often use to reduce swimming effort in natural conditions, and (b) stream fish are likely to be in better condition than laboratory fish.

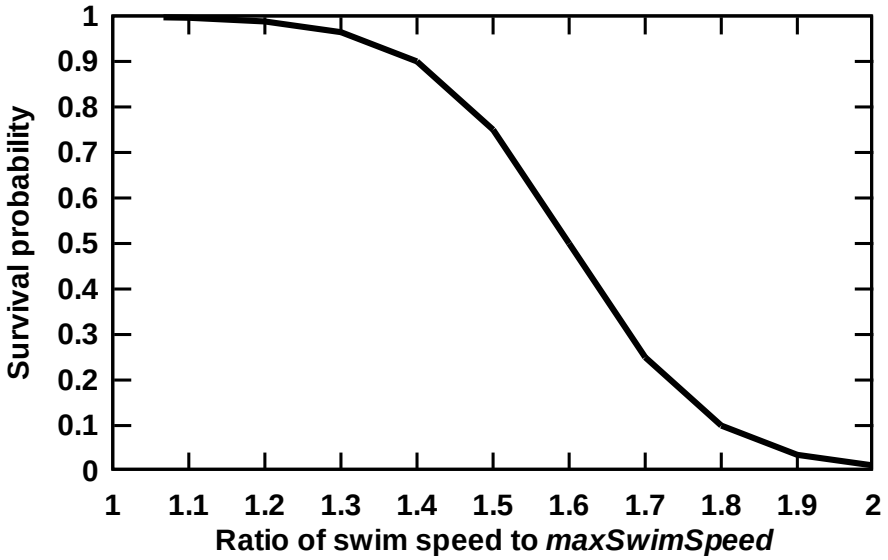

Figure 27. Survival probability function for high velocity. The X axis is the fish's actual swimming speed divided by its maximum sustainable swimming speed.

Table 13. Parameter values for high velocity mortality.

Parameter	Definition	Value
fishMaxSwimParamA	Length coefficient in maximum swim speed equation (1/s)	2.8
fishMaxSwimParamB	Constant in maximum swim speed length term (cm/s)	21
fishMaxSwimParamC	Temperature squared coefficient in maximum swim speed equation ($^oC^{-2}$)	-0.0029
fishMaxSwimParamD	Temperature coefficient in maximum swim speed equation ($^oC^{-1}$)	0.084
fishMaxSwimParamE	Constant in maximum swim speed temperature term (unitless)	0.37
mortFishVelocityV9	Ratio of fish swimming speed to maximum swim speed at which high velocity survival is 90 pct (unitless)	1.4
mortFishVelocityV1	Ratio of fish swimming speed to maximum swim speed at which high velocity survival is 10 pct (unitless)	1.8

7.4.3 Stranding

Stranding mortality represents the death of fish that are unable to move out of cells that become extremely shallow or dry as flow decreases. Fish in *inSALMO* already have a strong incentive to avoid cells with near-zero depth: drift food intake and survival of terrestrial predation are low. However, there can be cases where (a) a fish is limited by its maximum movement distance from reaching a cell with non-zero depth, or (b) no better habitat is available for other reasons.

Survival of stranding is modeled as an increasing logistic function of depth divided by fish length (Figure 28; Table 14). Because the terrestrial predation function does not represent the greatly increased likelihood of predation when depth is extremely low (e.g., when fish are trapped in isolated pools; Harvey and Stewart 1991), this risk is included as part of stranding mortality. The stranding survival function does not distinguish whether fish in very low or zero depths die from lack of water or from predation.

The stranding parameters do not cause survival to reach zero when depth is zero, reflecting that real habitat (as opposed to the model's cells) has variation in bottom elevation- some water could remain even if a cell's simulated depth becomes zero. Depth is divided by fish length to scale how the risks of low depths vary with fish size: shallow habitat that may be very valuable for small fish (protecting them from aquatic predation) may pose a stranding risk for large fish.

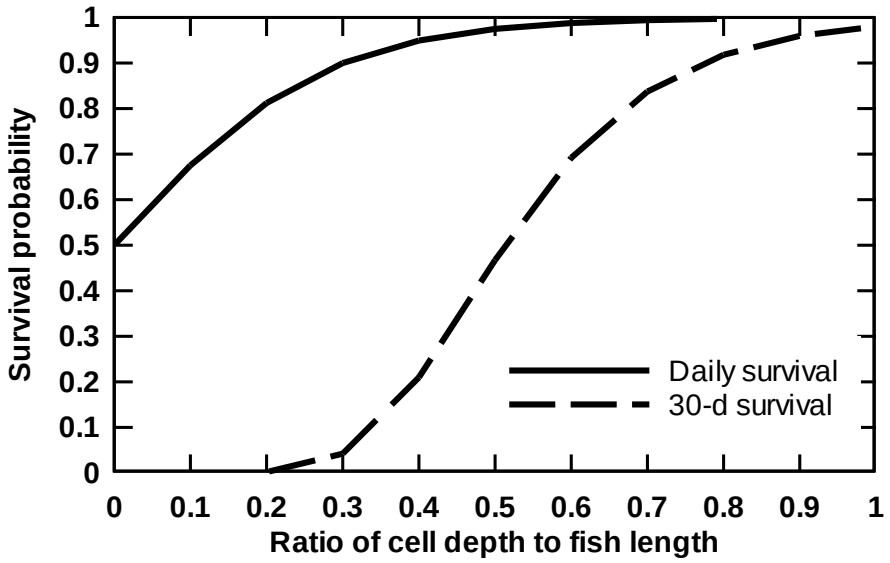

Figure 28. Survival probability function for stranding, showing the probability for surviving one day (solid line) and for 30 days (dashed line).

Table 14. Parameter values for stranding mortality.

Parameter	Definition	Units	Value
mortFishStrandD1	Ratio of depth to fish length at which stranding survival is 10 pct	none	-0.3
mortFishStrandD9	Ratio of depth at which stranding survival is 90 pct	none	0.3

7.4.4 Poor condition

Fish in poor condition (low value of the condition factor *K*, weight in relation to length; Section 7.3.1) are at risk of starvation, disease, and excess vulnerability to predators. These risks are combined in the poor condition survival probability. Simpkins et al. (2003a, b) studied starvation mortality in large juvenile trout, finding:

- Trout can survive for long periods (over 147 d, in some cases) with no food intake;
- Survival is lower at higher swimming activity and temperature (which both increase metabolism);
- Relative weight (equivalent to *K*) decreased linearly over time during starvation; but
- Mortality was predicted better by an index of lipid content than by *K*; one reason is that lipids are replaced by water as energy stores are depleted.

Unfortunately, modeling how body lipids are depleted and replaced by water and related processes would add considerable complexity and uncertainty to *inSALMO*, as they are not well understood. Instead, poor condition survival probability is represented as an increasing logistic function of *K* with parameter values estimated to provide reasonable survival probabilities over several days and weeks (Figure 29; Table 15). The parameters produce a survival probability less than 100 percent even when *K* is at its maximum of 1.0, because disease can occur (though is less likely) when condition is relatively good.

Poor condition is a unique mortality source in that fish can never increase their survival probability immediately by selecting different habitat. Fish in poor condition have a strong incentive to select habitat that provides rapid growth so their condition increases; however, sufficient growth to recover high condition takes a number of days. Even apparently high daily survival probabilities for this mortality source (e.g., 0.90) result in a low probability of surviving until normal weight can be regained. As Figure 29 indicates, the probability of surviving for extended periods becomes quite low when *K* falls below 0.8.

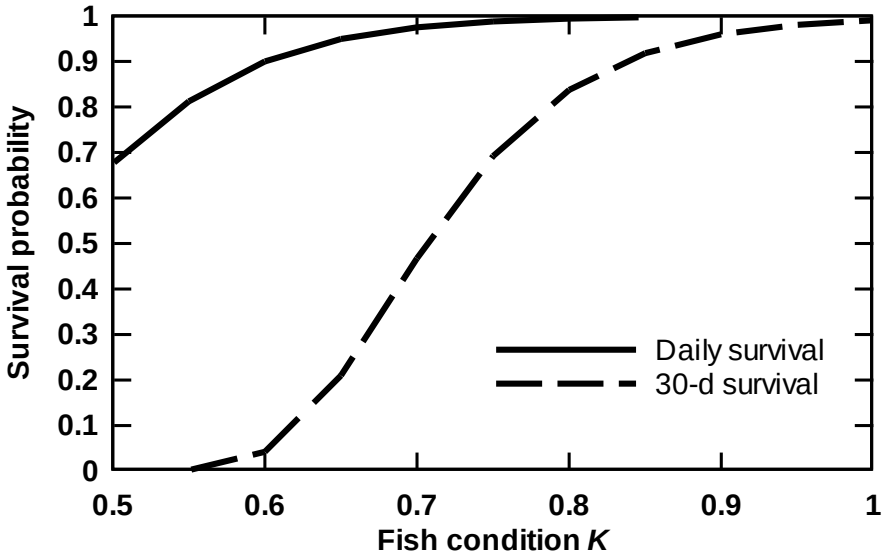

Figure 29. Survival probability function for poor condition. The dotted line is the probability for surviving for 30 d at the value of *K*.

Table 15. Parameter values for poor condition mortality.

Parameter	Definition	Value
mortFishConditionK1	Fish condition factor *K* at which survival is 10 pct (unitless)	0.3
mortFishConditionK9	*K* at which survival is 90 pct (unitless)	0.6

Before modifying the parameters for poor condition, users of *inSALMO* should be aware that poor condition mortality can have a strong effect on habitat selection (Section 7.2.2) as well as mortality. As a consequence, changes in parameter values are likely to have widespread, complex, and unexpected effects. For example, one might assume that increasing the survival probability (e.g., by decreasing *mortFishConditionK9* from 0.6 to 0.7) would result in less mortality due to poor condition. However, because fish select habitat using a tradeoff between poor condition and other (primarily, predation) mortality sources, this change in parameters could result in fish selecting different habitat that has lower growth and lower predation risk, at least partially offsetting the expected reduction in poor condition mortality.

7.4.5 Terrestrial predation

Predation by terrestrial animals is a dominant source of mortality to salmon, especially adults (Alexander 1979, Harvey and Marti 1993, Metcalfe et al. 1999, Quinn and Buck 2001, Valdimarsson et al. 1997). The terrestrial predation formulation represents predation by a mix of such predators as otters, raccoons, snakes, herons, mergansers, kingfishers, and dippers.

Characteristics of terrestrial predators that affect the survival probability function include they generally (but not always):

- Are bigger than salmon,
- Are poorer swimmers than relatively large salmonids,
- Are warm-blooded, and
- Locate fish prey from the air.

These characteristics vary among predators, but they lead to these generalizations about terrestrial predation:

- Big salmon are vulnerable, often more vulnerable than very small salmon;
- Risks are year-round because warm-blooded predators feed as much or more in winter (except those that hibernate or migrate); and
- Salmon are more at risk when more visible from the air.

Results of the *inSTREAM* individual-based trout model, which uses the same formulation as *inSALMO* for predation survival, are quite sensitive to how terrestrial predation varies with habitat variables such as depth and velocity. Results of *inSALMO* are expected to be less sensitive to terrestrial predation because (a) adult salmon are only present for short times, so predation risk does not control their abundance, and (b) juveniles are still vulnerable to terrestrial predation but likely much more vulnerable to predation by other fish—at least at sites where where non-salmonid predators such as pikeminnow and bass are abundant.

The formulation assumes a minimum survival probability that applies when fish are most vulnerable to terrestrial predation, and a number of "survival increase functions" that can increase the probability of survival above this minimum. Survival increase functions have values between zero and one, with higher values for greater protection from predation. The survival increase functions are assumed to act independently. Therefore, the terrestrial predation survival probability (terrPredSurv) is obtained by increasing the minimum survival (decreasing the difference between minimum survival and 1.0) by the maximum of the independent survival increase functions. This assumption is expressed mathematically as:

$$terrPredSurv = mortFishTerrPredMin + [(1 - mortFishTerrPredMin) \times \max(terrPredDepthF, terrPredTurbidityF, terrPredLengthF \ldots)].$$

where *terrPredDepthF*, *terrPredTurbidityF*, etc. are the values of the survival increase functions described below.

Using this approach, the value of *terrPredSurv* does not vary with how many survival increase functions there are, but instead is only limited by one function at a time. Survival increase functions can be added, removed, or revised without re-calibrating the overall predation survival rate. However, the approach does not represent the potential combined effects of, for example, using deeper and faster habitat. Both depth and velocity make fish more difficult to see, and the combination of deep and fast is safer than only deep or fast; but this combined effect is not represented in this formulation.

The value of *mortFishTerrPredMin* is assumed to be the daily probability of surviving terrestrial predation under conditions where the survival increase functions are minimal (offering no reduction in risk). Field data for estimating this minimum survival are unlikely to be available, so it is best estimated by calibrating the model to observed abundance and habitat use patterns.

The following survival increase functions are included. (The effect of any function can be turned off by setting its function's parameters to yield values near zero.) Suggested parameter values are provided at the end of the section (Table 16).

Depth. Fish are more vulnerable to terrestrial predators when in shallow water, where they are easier for predators to locate and catch. The depth survival increase function is an increasing logistic curve: survival increases as depth increases (Figure 30). Power (1987) indicates that predation by birds is low at depths above 20 cm, and Hodgens et al. (2004) report that 85% of successful strikes by herons were at depths less than 20 cm but some were at depths up to 50 cm. However, predators that are larger or better swimmers (mergansers, otters) are effective at greater depths, especially in clear water. (Note that the very high risk of terrestrial predation that occurs when fish are in near-zero depths is included in stranding mortality.)

Appropriate values for the depth survival increase function parameters can differ among sites. Parameters useful in relatively small streams of coastal California (Railsback and Harvey 2001) provide high relative survival in depths > 1 m. However, these parameters were not useful for the much larger Green River in Utah, where depths can be several meters and otters are prevalent; separate parameters were developed for the Green River site. Figure 30 illustrates parameter values for small streams and large rivers (Table 16).

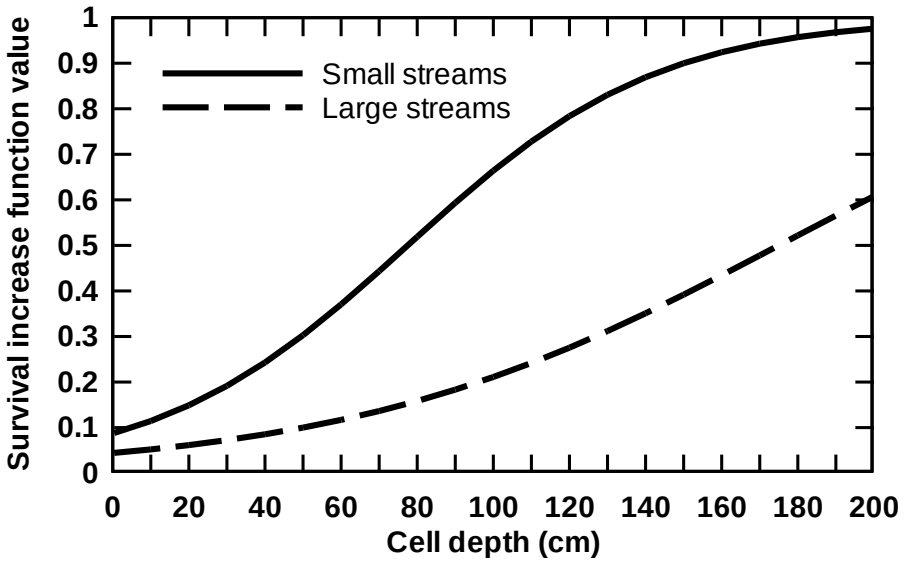

Figure 30. Depth survival increase function for terrestrial predation survival.

Turbidity. Turbidity makes fish less visible to terrestrial predators and, because detection from the air is key to terrestrial predation success, is assumed to be an important survival increase function. No literature directly relating terrestrial predation to turbidity was found. Instead, this formulation considers the observed effect of turbidity on the ability of fish to detect prey

(Section 7.3.3), which shows the ability to detect drifting invertebrates declining toward zero at 40 NTUs. Fish are likely more visible than invertebrates because of their size, but terrestrial predators must observe prey through greater lengths of water than must fish predators. Therefore, the turbidity survival increase function has little effect at values below 5 NTUs but strongly reduces terrestrial predation risk at >40 NTUs (Figure 31).

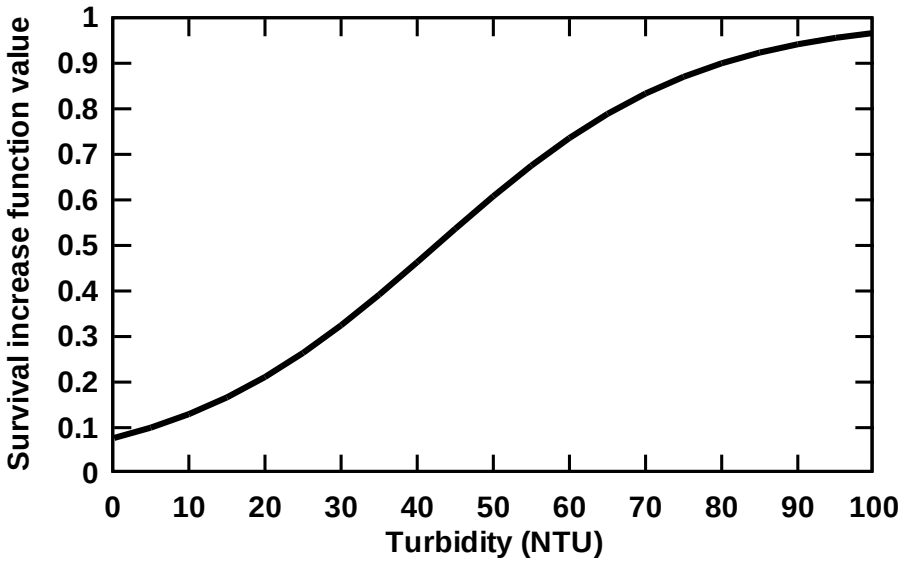

Figure 31. Turbidity survival function for terrestrial predation survival.

Fish length. Small fish are less vulnerable to terrestrial predation, presumably because they are less visible (Power 1987), less desirable, and possibly more difficult to capture, than larger fish. For example, Hodgens et al. (2004) reported that 48 trout eaten by heron ranged 3-38 cm in length, but 85% were between 10 and 28 cm. Dippers (*Cinclus mexicanus*) are an example terrestrial predator that selects salmonid fry and other small fish (Thut 1970), so very small fish are not invulnerable to terrestrial predation. Therefore, survival of terrestrial predation is assumed to decrease with fish length, but only fish less than 4 cm in length are relatively protected (Figure 32). These parameter values should be reconsidered for sites where predation is dominated by larger mammals (otters, bears) that strongly prefer large fish.

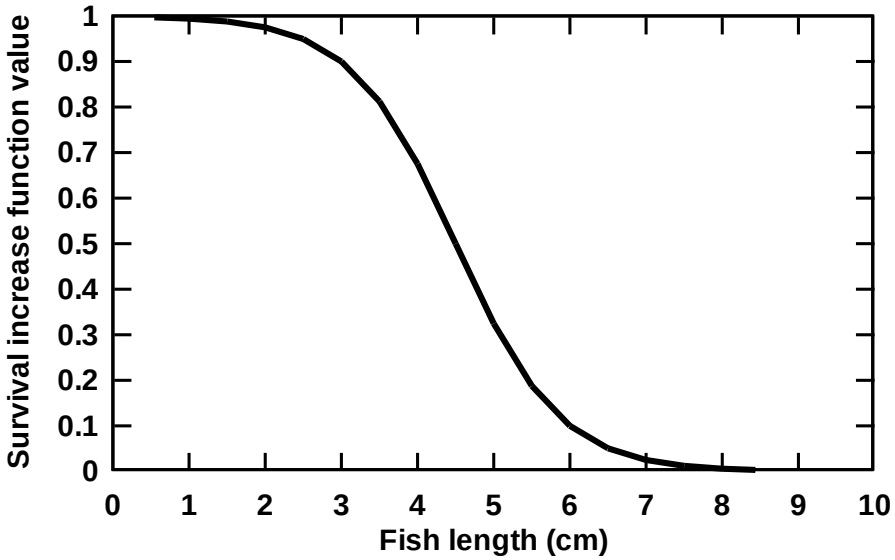

Figure 32. Fish length survival increase function for terrestrial predation survival.

Feeding time. Fish are much more vulnerable to predation when they are actively feeding during the day instead of resting and hiding at night (Metcalfe et al. 1999). The survival increase function is modeled as a decreasing function of *feedTime* (h), the hours spent feeding per day (Section 7.3.2). Parameters are chosen so survival decreases nearly linearly with feedTime (Figure 33).

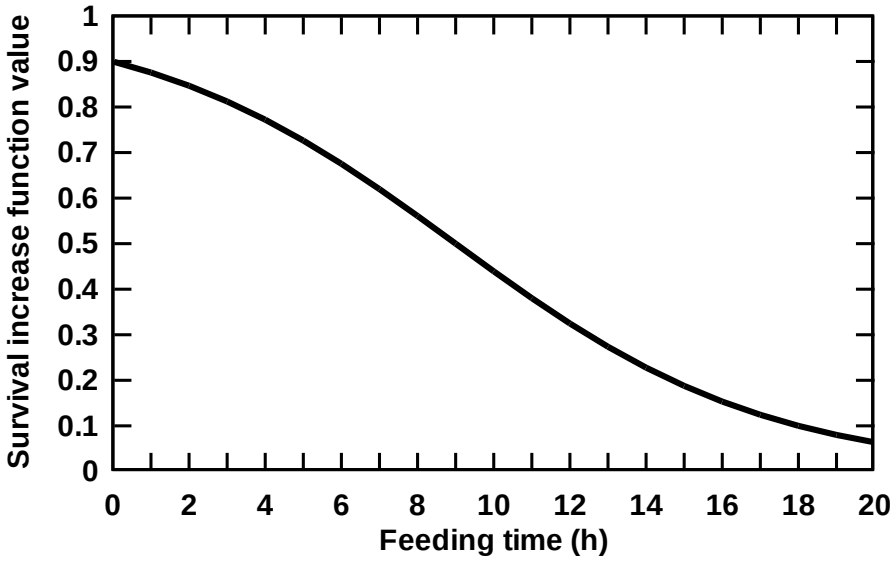

Figure 33. Feeding time function for terrestrial predation mortality.

Water velocity. Water velocity is assumed capable of increasing terrestrial predation survival because (1) velocity-caused turbulence makes fish harder to see, and (2) some predators are poorer swimmers than salmon so they are expected to be less able capture fish in faster water.

The survival increase function is therefore an increasing logistic curve that provides sharply increasing protection from terrestrial predators at velocities above 50 cm/s (Figure 34). As with the depth survival increase function, useful parameter values for the velocity function may differ between small and large streams. In small streams, high velocities combine with high turbulence and obstacles to make swimming difficult. In large rivers, however, there can be run habitat where velocities are high while turbulence is low, so good swimmers such as mergansers and otters may perform quite well. Two sets of parameter values are provided in Table 16 and illustrated in Figure 34.

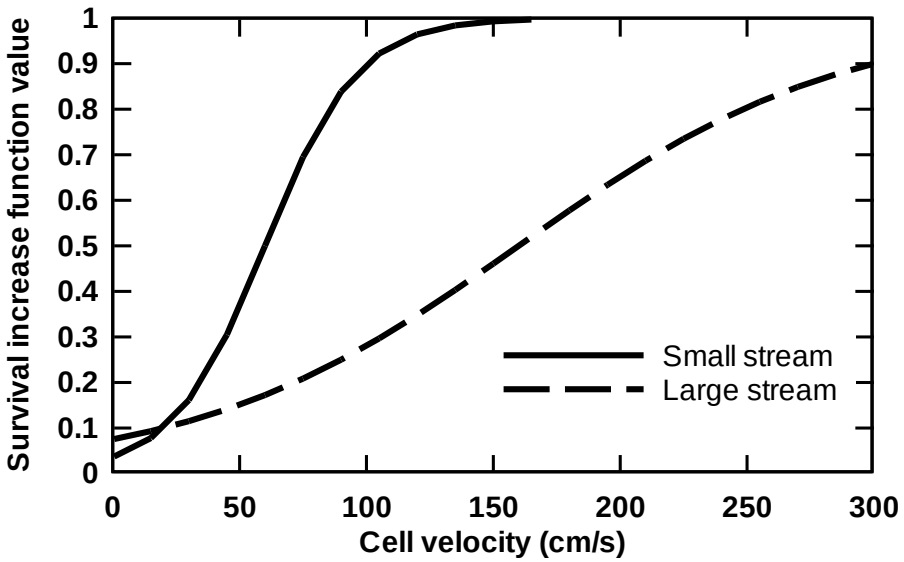

Figure 34. Velocity survival increase function for terrestrial predation survival, with parameters for both small streams and large rivers.

Temperature. No temperature-based survival increase function is included in *inSALMO* because there are no clear mechanisms that would cause terrestrial predation pressure (unlike fish predation) to change with temperature. There is not a good basis for assuming predator activity is lower in winter; most important terrestrial predators are warm-blooded and many do not hibernate. In fact, such predators need additional food to maintain their metabolic needs in winter. The reduced swimming ability of salmon at low temperatures can also offset any decreased activity by predators by reducing the ability of salmon to escape (Metcalfe et al. 1999). Terrestrial predation can be greatly reduced when rivers freeze over, but ice is not represented in *inSALMO*.

Distance to hiding cover. Fish can avoid mortality by hiding when predators are detected. The success of this tactic depends on the presence of hiding cover and the distance the fish must travel to reach it. The value of hiding cover is one habitat function that clearly occurs at a spatial scale different from the cell size typically used in *inSALMO*; hiding cover several to tens of meters from a fish can provide at least some predation protection.

Hiding cover is represented with a survival increase function that increases as distance to hiding cover decreases. Distance to cover (*cellDistanceToHide*, cm) is an input for each habitat cell, estimated in the field as the average distance a fish in the cell would need to move to hide from a predator. The value of *cellDistanceToHide* can range from near zero, for cells where a bottom of boulders or vegetation provides almost continuous cover, to many meters for cells lacking bottom cover and far from the banks (e.g., extensive gravel bars). Very short distances to hiding cover (< 100 cm) provide nearly complete protection from some predators, but do not protect fish from predators that strike very quickly (e.g., some birds) or that could be able to extract salmon from hiding (e.g., otters). Cover several meters away is still valuable for escaping from terrestrial predators that have been detected. Therefore, the effect of distance to hiding cover is modeled as a decreasing logistic function of *cellDistanceToHide* (Figure 35).

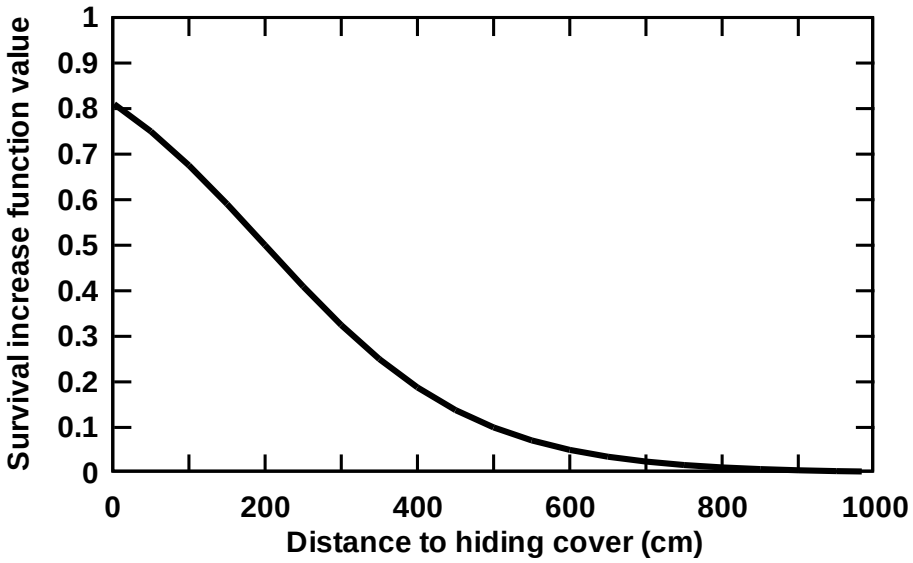

Figure 35. Distance to hiding cover function for terrestrial predation survival.

Table 16. Parameter values for terrestrial predation mortality. Values are estimates for mid-sized spawning streams and should be re-considered for each site.

Parameter	Definition	Value
mortFishTerrPredMin	Daily survival probability due to terrestrial predators under most vulnerable conditions (unitless)	0.99 (until fit via calibration)
mortFishTerrPredD1	Depth at which survival increase function is 10 pct of maximum (cm)	5
mortFishTerrPredD9	Depth at which survival increase function is 90 pct of maximum (cm)	200
mortFishTerrPredL9	Fish length at which survival increase function is 90 pct of maximum (cm)	3
mortFishTerrPredL1	Fish length at which survival increase function is 10 pct of maximum (cm)	6
mortFishTerrPredF9	Feeding time at which survival increase function is 90 pct of maximum (h)	0
mortFishTerrPredF1	Feeding time at which survival increase function is 10 pct of maximum (h)	18
mortFishTerrPredV1	Velocity at which survival increase function is 10 pct of maximum (cm/s)	20
mortFishTerrPredV9	Velocity at which survival increase function is 90 pct of maximum (cm/s)	200
mortFishTerrPredH9	Distance to hiding cover at which survival increase function is 90 pct of maximum (cm)	-100
mortFishTerrPredH1	Distance to hiding cover at which survival increase function is 10 pct of maximum (cm)	500
mortFishTerrPredT1	Turbidity at which survival increase function is 10 pct of maximum	10
mortFishTerrPredT9	Turbidity at which survival increase function is 90 pct of maximum	50

7.4.6 Aquatic predation

The aquatic predation formulation represents mortality due to predation by fish. This formulation has been modified from that of *inSTREAM* (Railsback et al. 2009) by removing the assumption that the dominant source of aquatic predation is cannibalism. Instead, inSALMO assumes that juvenile salmon are vulnerable to predation by an unspecified community of predatory fish and that the predation risk is unrelated to the simulated salmon population.

As with terrestrial predation, the formulation uses a minimum survival probability that applies when fish are most vulnerable to aquatic predation, and a number of survival increase functions.

$$aqPredSurv = mortFishAqPredMin + [(1 - mortFishAqPredMin) \times \max(aqPredDepthF, aqPredLengthF, aqPredVelF \ldots)]$$

where *aqPredSurv* is the daily survival probability for a particular fish in a particular habitat cell and *aqPredDepthF*, *aqPredLengthF*, etc. are survival increase function values. The value of *mortFishAqPredMin* is the daily probability of surviving aquatic predation under conditions where the survival increase functions offer no reduction in risk. As with terrestrial predation, data for directly estimating aquatic risks are unlikely to be available, so it is recommended that *mortFishAqPredMin* be estimated by calibrating the model to observed patterns of abundance and habitat selection by juvenile fish.

The aquatic predation survival formulation includes the following functions for survival increase functions. Parameter values are given at the end of the section (Table 17).

Distance to hiding cover. Salmon juveniles are assumed to use hiding cover to avoid fish as well as terrestrial predators, so a survival increase function for cell distance to hiding cover is included. (This is a change from the trout model formulation of Railsback et al. 2009.) The hiding cover formulation has the same form as that for terrestrial predation, a decreasing logistic function of *cellDistanceToHide* (Figure 35). Separate parameters (*mortFishAqPredH9*, *mortFishAqPredH1*) are used to define the hiding cover function for aquatic predation, so it can have a different shape than that for terrestrial predation. The hiding cover parameters for aquatic predation were chosen to represent the assumptions that, for small salmon, hiding cover must be quite close to provide protection from fish, and that even dense cover does not provide complete protection from smaller predators such as trout.

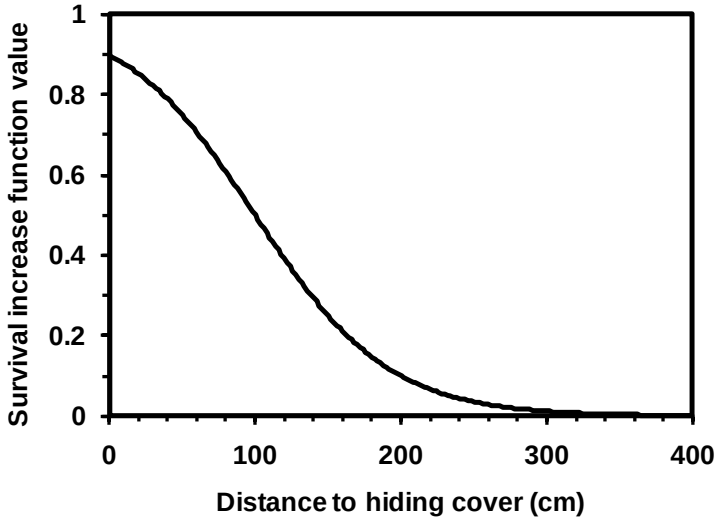

Figure 36. Hiding cover survival increase function for aquatic predation.

Depth. Aquatic predation survival is assumed to be high in water shallow enough to physically exclude large fish, or shallow enough to place large fish at high risk of terrestrial predation. The

depth survival increase function is therefore a decreasing logistic function, with high survival at depths less than 5 cm (Figure 37).

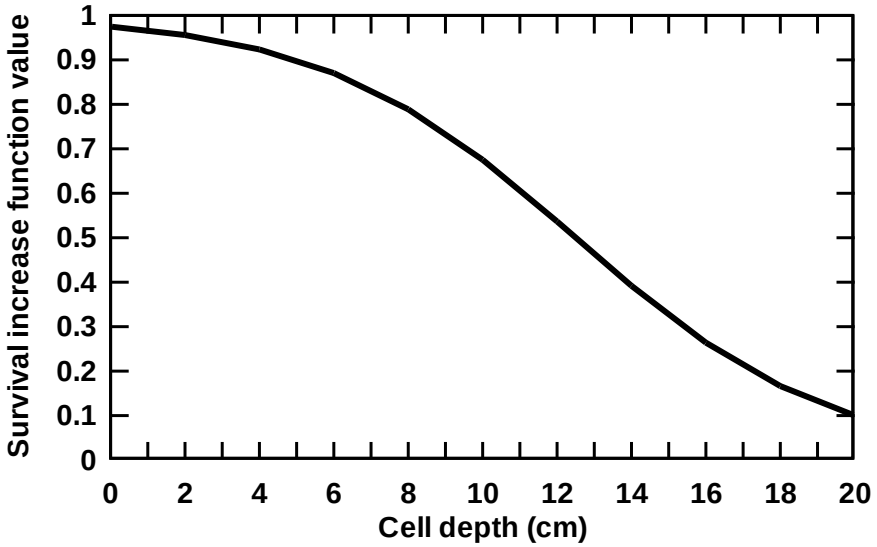

Figure 37. Depth survival increase function for aquatic predation survival.

Fish length. As fish grow, they become better able to out-swim piscivorous fish and fewer piscivorous fish are big enough to swallow them. The length survival increase function is therefore an increasing logistic function, the parameters for which depend on the size of the piscivorous fish. Keeley and Grant (2001) provide an empirical relation between the size of piscivorous stream trout and the size of their fish prey. Figure 38 illustrates parameters for sites where the predator fish community includes large-gaped piscivores such as pikeminnow and bass.

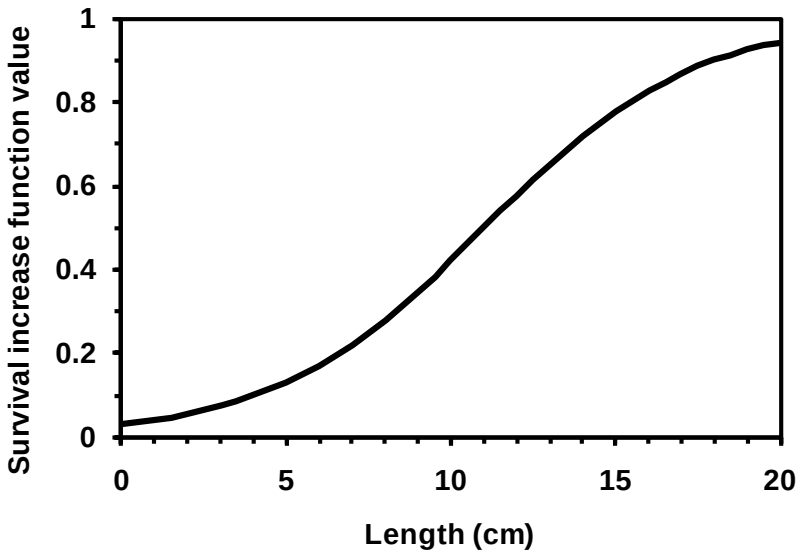

Figure 38. Fish length survival increase function for aquatic predation survival.

Feeding time. This survival increase function is the same for aquatic predation as it is for terrestrial predation. The survival increase is a decreasing logistic function of *feedTime*, the number of hours per day spent foraging. Separate parameters control the feeding time function for aquatic vs. terrestrial predation, but the values recommended above for terrestrial predation are also recommended for aquatic predation.

Low temperature. This survival increase function reflects how low temperatures reduce the metabolic demands, swimming ability, and, therefore, feeding activity of piscivorous fish. The function is a decreasing logistic function (Figure 39) that approximates the decline in metabolism and feeding with temperature of a mixed community of warmwater (e.g., pikeminnow) and coldwater (e.g., trout) predators.

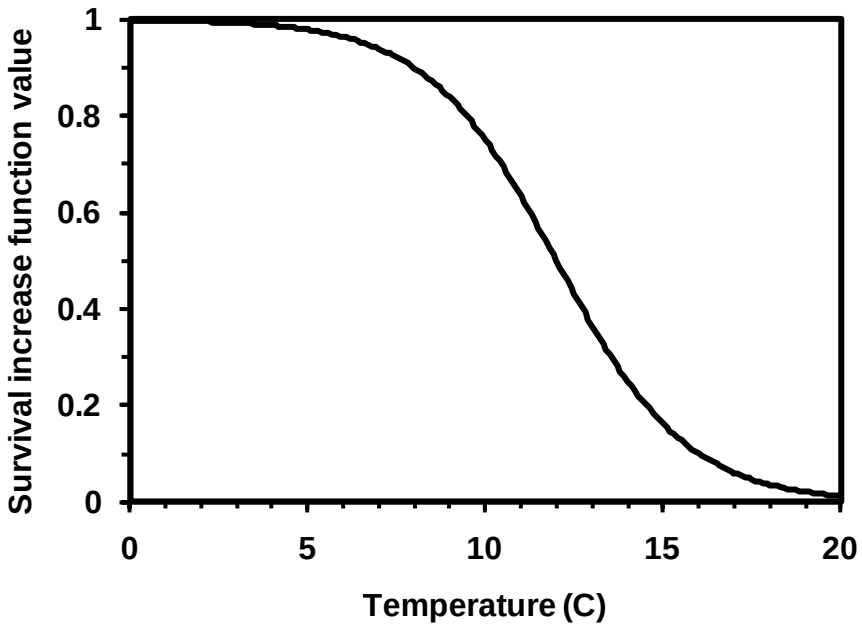

Figure 39. Temperature survival increase function for aquatic predation survival.

Turbidity. The survival increase function for turbidity represents how encounter rates between predator and prey fish decline as turbidity increases. The turbidity function is based on experimental observations and citations provided by Gregory and Levings (1999). Gregory and Levings compared piscivory by fish in adjacent clear and turbid rivers and found piscivory much lower, but still present, in the turbid river. Turbidity appears to reduce the ability of piscivorous fish to detect prey fish and thus the encounter rate between predator and prey (Gregory and Levings 1999, Vogel and Beauchamp 1999, DeRobertis et al. 2003). One mechanism that can offset this reduced encounter rate is that turbidity also reduces the vulnerability of piscivorous fish to terrestrial predation, making them more likely to forage in shallow habitat where small fish are likely to be found (Vogel and Beauchamp 1999). The parameters for this function provide no protection from aquatic predation at low turbidities and a 50 percent reduction in risk at 40 NTU (Figure 40). As turbidity continues to increase toward extreme values, aquatic predation risk continues to decrease but is not eliminated.

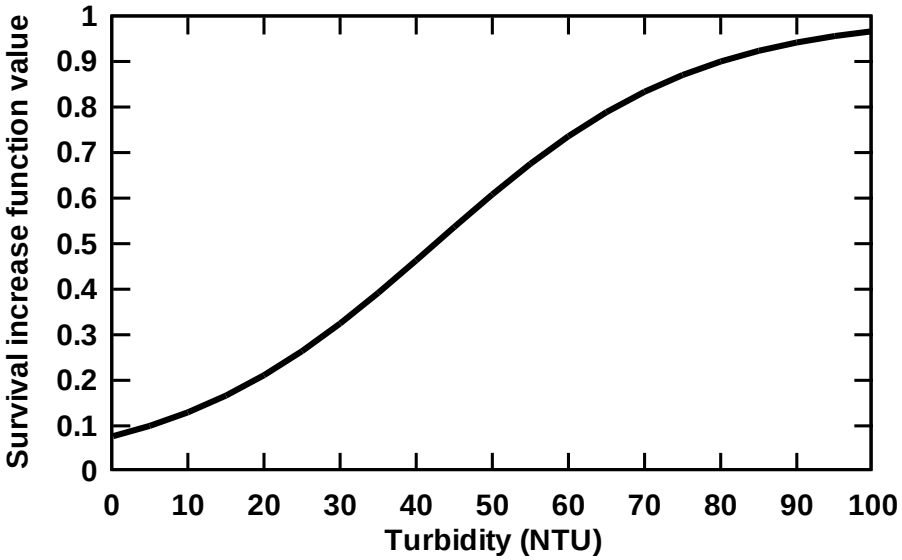

Figure 40. Turbidity survival increase function for aquatic predation survival.

Table 17. Parameter values for aquatic predation mortality. Parameter values are for sites where large-gaped, warm- and coldwater predators are abundant.

Parameter	Definition	Value
mortFishAqPredMin	Daily survival probability due to aquatic predators under most vulnerable conditions (unitless)	0.9 (until fit via calibration)
mortFishAqPredH9	Distance to hiding cover at which survival increase function is 90 pct of maximum (cm)	0
mortFishAqPredH1	Distance to hiding cover at which survival increase function is 10 pct of maximum (cm)	200
mortFishAqPredD9	Depth at which survival increase function is 90 pct of maximum (cm)	10
mortFishAqPredD1	Depth at which survival increase function is 10 pct of maximum (cm)	20
mortFishAqPredL1	Fish length at which survival increase function is 10 pct of maximum (cm)	4
mortFishAqPredL9	Fish length at which survival increase function is 90 pct of maximum (cm)	18
mortFishAqPredF9	Feeding time at which survival increase function is 90 pct of maximum (h)	0
mortFishAqPredF1	Feeding time at which survival increase function is 10 pct of maximum (h)	18
mortFishAqPredT9	Temperature at which survival increase function is 90 pct of maximum (°C)	8
mortFishAqPredT1	Temperature at which survival increase function is 10 pct of maximum (°C)	16
mortFishAqPredU9	Turbidity at which survival increase function is 90 pct of maximum (NTU)	80
mortFishAqPredU1	Turbidity at which survival increase function is 10 pct of maximum (NTU)	5

7.4.7 Demonic intrusion: experimenter-induced mortality

The graphical interface of *inSALMO*'s software allows the user to select individual salmon and remove them from the simulation. This capability can be useful for conducting controlled simulation experiments (e.g., Railsback and Harvey 2002 used it to look at how a hierarchy of adult trout shifted as the largest individuals were removed). Fish that are killed by the experimenter in this way are labeled as having died of "demonic intrusion", a term used by Hurlbert (1984) for the effects of experimenters on their study systems. There are no parameters

or equations related to demonic intrusion mortality, but it appears as a potential mortality source in model output.

8 inSALMO Model Description: Redds

Redds are the nests laid by spawning salmon. In *inSALMO*, a redd and the eggs it contains are modeled as one object: individual fish are not tracked until they emerge. The model redds keep track of the number of eggs remaining alive and determine when the eggs turn into new salmon. The species of a redd and its initial number of eggs are determined by the female spawner that created the redd (Section 7.1.3).

Because of its objectives as a management model, *inSALMO* models redds with relatively little biological detail but with substantial detail in how stream flow and temperature affect egg incubation and survival. The following are among the processes that can affect salmonid spawning success (see, e.g., Groot and Margolis 1991) that are not considered explicitly in *inSALMO*.

- Eggs can be killed by a variety of predators and parasites.
- Gravel size, fine sediment, and water quality can affect egg survival and development rates. In particular, low flow of water through the redd can allow metabolic wastes to accumulate and kill eggs. Deposition of fine sediment can prevent newly hatched fish from emerging.
- Salmonids go through several life stage transformations while in their redds. The most important of these is the transformation from eggs into alevins, which have respiratory and movement capabilities and, hence, different vulnerability to being dewatered.

Redds are modeled using the following four daily actions. Scheduling of these actions is discussed in Section 11.

8.1 Survival

In *inSALMO*, eggs incubating in a redd are subject to five mortality sources: low and high temperatures, scouring by high flows, dewatering, and superimposition (having another redd laid on top of an existing one). Redd survival is modeled using redd “survival functions”, which determine, for each redd on each day, the probability of each egg surviving one particular kind of mortality. Then, a random draw is made on a binomial distribution to determine how many eggs survive each redd mortality source. A binomial distribution is a statistical model of the (integer) number of occurrences of some event within a specified number of trials, when the probability of occurrence per trial is known. In this case, the event is death of one egg, the number of trials is the number of eggs in the redd, and the probability of occurrence is one minus the survival function value. Hence, the binomial distribution returns a randomly drawn number of eggs that die, given the number of live eggs and the per-egg mortality probability. (The alternative approach of multiplying the mortality probability by the number of live eggs may appear simpler, but introduces a number of numerical difficulties when the number of live eggs is small.)

The separate redd mortality sources are executed sequentially: the eggs killed by one source are subtracted from the number alive before the next source is processed. The order in which redd survival functions are evaluated is defined in Section 11.3.

The kinds of mortality represented, and the survival function methods, were selected considering that the objectives of *inSALMO* focus on flow and temperature effects on salmon populations. Consequently, the methods are simple and focussed on temperature and flow effects. For example, there is no redd survival function related to spawning gravel quality. Spawning gravel quality has several effects on redd success (Kondolf 2000) but *inSALMO* is not designed address to represent gravel quality issues. [The spawning site selection criteria (Section 7.1.2) allow a fish to spawn in a cell that has little or no gravel; there is no redd mortality penalty for doing so. The exception is that if superimposition occurs in a cell with little spawning gravel (unlikely unless gravel is rare) then superimposition mortality is likely to be high.] For several of the redd mortality sources (especially, dewatering and superimposition), more detailed and mechanistic approaches are available in the literature and could be added to *inSALMO* in situations where these mortality sources are believed to be important.

8.1.1 Dewatering

Dewatering mortality occurs when flow decreases until a redd is no longer submerged; eggs can be killed by dessication or the buildup of waste products that are no longer flushed away. Reiser and White (1983) did not observe significant mortality of eggs when water levels were reduced to 10 cm below the egg pocket for several weeks. However, they also cited literature indicating high mortality when eggs and alevins are only slightly submerged (which may yield poorer chemical conditions than being dewatered), and high mortality for dewatered alevins. Because *inSALMO* does not distinguish between eggs and alevins, these processes are not modeled mechanistically or in detail. The dewatering survival function is simply that if depth is zero then the daily fraction of eggs surviving is equal to the fish parameter *mortReddDewaterSurv*. This parameter has a suggested value of 0.9, which reflects the variability in dewatering effects. Egg survival may be high when a redd is first dewatered, so *mortReddDewaterSurv* should not be too low.

8.1.2 Scouring and deposition

Scouring and deposition mortality results from high flows disturbing the gravel containing a redd. If eggs are scoured out of a redd, they likely to be washed downstream and are vulnerable to being eaten. Deposition of new gravel on top of a redd may make water flow through the redd inadequate to transport oxygen and waste materials, or may prevent newly hatched salmon from emerging. Deposition is especially likely to reduce survival if it includes fine sediment.

There are empirical methods for predicting the potential for scouring as a function of shear stress and substrate particle size at the local scale of a habitat cell, but geomorphologists now understand that scour and deposition at the scale of individual redds is a highly variable process best represented as stochastic. At least in gravel-bed streams, it is virtually impossible to predict where scour and deposition will occur at various flows (Haschenburger 1999, Wilcock et al. 1996). Consequently, *inSALMO* adopts an approach for predicting the probability of redd scouring or deposition from the empirical, reach-scale work of Haschenburger (1999). This approach was developed for gravel-bed channels and may not be appropriate for sites where spawning gravels occur mainly in pockets behind obstructions (where scouring is likely even less

predictable). *inSALMO* should be considered substantially more uncertain for sites where populations are strongly limited by redd scouring, especially if spawning is limited to pocket gravels.

Haschenburger (1999) observed the spatial distribution and depth of scouring and deposition at a number of flow peaks in several study sites in gravel-bed rivers. The proportion of a stream reach that scoured or filled to a specified depth during a high-flow event was found to follow an exponential distribution, the parameter for which (*scourParam*) varies with site-average dimensionless (Shields) shear stress. Therefore, *inSALMO* assumes that the probability of a redd being destroyed is equal to the proportion of the stream reach scouring or filling to depths greater than the value of the fish parameter *mortReddScourDepth* (cm). Consequently, the probability of a redd *not* being destroyed (*scourSurvival*) is equal to the proportion of the stream scouring or filling to a depth less than the value of *mortReddScourDepth*. This scour survival probability is estimated from the exponential distribution model of Haschenburger (1999); the proportion of the stream scouring to less than a given depth is the integral of the exponential distribution between zero and the depth:

$$scourSurvival = 1 - e^{-scourParam \times mortReddScourDepth}.$$

(The value of *scourSurvival* is set to 1.0 if *scourParam*×*mortReddScourDepth* is greater than 100. This allows users to effectively turn scouring and deposition mortality off by using a very large value of *mortReddScourDepth*, e.g., 10,000 cm, without risk of the exponential function producing a variable underflow.)

The value of *scourParam* was modeled by Haschenburger empirically:

$$scourParam = 3.33 \times e^{-1.52 \times (shearStress/0.045)}.$$

where *shearStress* is the peak Shields stress (measured at a reach scale) occurring during the high-flow event. Shields stress is a dimensionless indicator of scour potential often used in modeling sediment transport, described in the sediment transport literature. Shields stress increases with flow, a relationship represented in *inSALMO* by the equation:

$$shearStress = habShearParamA \times flow^{habShearParamB}$$

where *habShearParamA* (s/m^3) and *habShearParamB* (unitless) are habitat reach parameters. These are habitat parameters because they are highly specific to each reach. Methods for estimating *habShearParamA* and *habShearParamB* are discussed in Section 16.7.2 of Railsback et al. (2009).

The fish parameter *mortReddScourDepth* can be evaluated as the egg burial depth, the distance down from the gravel surface to the top of a redd's egg pocket. Scour to this depth is almost certain to flush eggs out of the redd. Deposition of new material to this distance would double the egg pocket's depth, likely to severely reduce the survival and emergence of its eggs. DeVries (1997) reviews egg burial depths for stream salmonids. A value of 20 cm is reasonable for Chinook salmon.

Example scour survival parameters for a medium-gradient site with average gravel size of 3.5 cm (*habShearParamA* = 0.013, *habShearParamB* = 0.40, *mortReddScourDepth* = 20 cm) produce the relation between peak flow and probability of redd scouring illustrated in Figure 41.

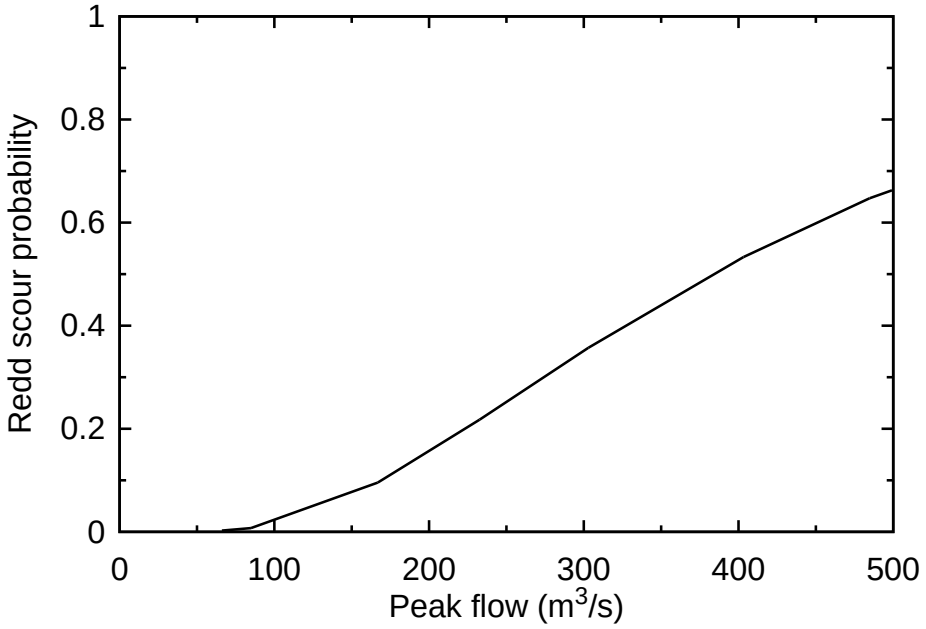

Figure 41. Example redd scour and fill survival function. The Y axis is the probability of a redd being destroyed during a peak flow event.

This model of scouring estimates the probability of a redd surviving scour in each high-flow event, not on a daily time step. The single survival probability is applied to all redds, assuming that if scouring occurs, then no eggs survive. [It is important to note that *inSALMO* calculates scouring survival from daily mean flows, whereas Haschenburger (1999) based her model on instantaneous peak flows. This approximation is made to avoid needing to input daily peak flows, but will cause scouring mortality to be underestimated when runoff is rapid.] The following steps are used for each redd, on each day.

- Determine whether the current day's flow in the redd's reach is greater than both the previous day's and the following day's flow. If so, then the following steps are conducted. If not, then the fraction of eggs surviving is 1.0 (no eggs are lost).

- Calculate the value of *scourSurvival*, using the above equations and the current day's flow for the redd's reach.

- Draw a uniform random number between zero and one. If the value of this random number is greater than the value of *scourSurvival*, then the fraction of eggs surviving is zero. Otherwise, the fraction of eggs surviving is 1.0.

To avoid the need for flow data for the date preceeding the start of a model run, redd scour is not executed on the first day of a run. However, redd scour can be executed on the last day, so flow input must extend at least one day past the last simulation date.

(Section 6.1.1 concerning flow input includes a potentially important note about using daily peak instead of mean flows to more accurately represent redd scour.)

8.1.3 Low temperature

Both low and high temperatures cause mortality in eggs, at temperatures much different than those causing mortality in fish. Mortality due to high and low temperatures are modeled separately. Logistic functions represent the available data well.

The daily fraction of eggs surviving low temperatures is modeled as an increasing logistic function of temperature. Parameter values appear to differ among species, with differences especially likely between species (or stocks) that spawn in the fall v. spring. In developing parameter values from published data on egg survival, it is important to remember that eggs incubate slowly at low temperatures, so even apparently high daily survival rates can result in low egg survival over the entire incubation period. Parameter values for fall Chinook salmon (Table 18; Figure 42) have been determined from data compiled by Myrick and Cech (2004).

Table 18. Parameter values for low temperature redd mortality.

Parameter	Definition	Species	Value
mortReddLoTT1	Temperature at which low temperature survival of eggs is 10 pct (°C)	Chinook	1.7
mortReddLoTT9	Temperature at which low temperature survival of eggs is 90 pct (°C)	Chinook	4.0

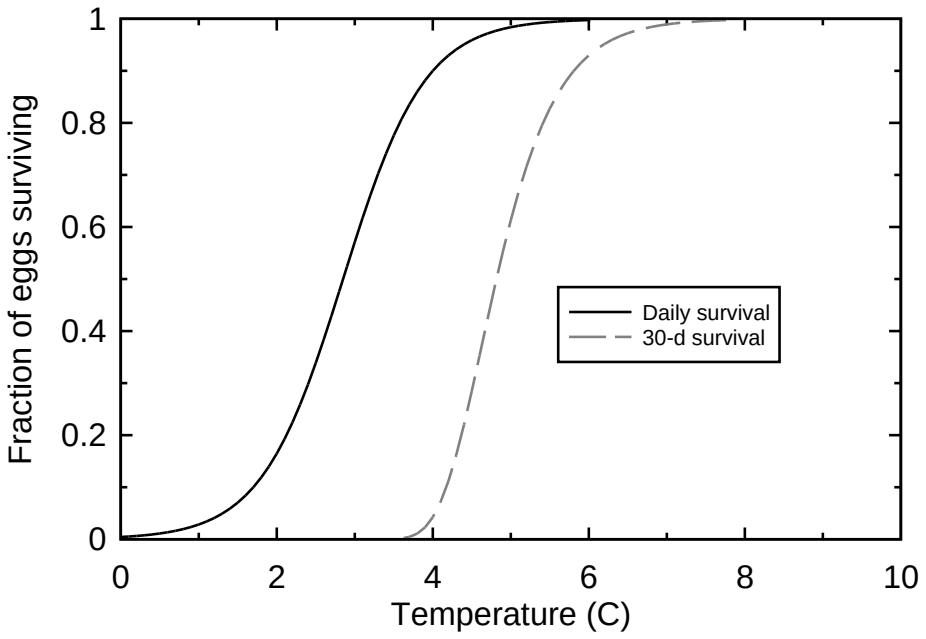

Figure 42. Low temperature redd survival function, for fall Chinook salmon parameter values.

8.1.4 High temperature

High temperatures can induce direct mortality in trout eggs, and also promote fungus and disease. The fraction of eggs surviving high temperatures is modeled as a decreasing logistic function of temperature (Figure 43). Parameter values for Chinook salmon were estimated to reproduce several patterns summarized from the literature by Myrick and Cech (2004): temperature effects become detectable around 12°, mortality is clear but not rapid by 14°, and mortality is strong and rapid by around 16.5°. The parameter values (Table 19) appear to indicate high survival at high temperatures, but in fact cause low survival if temperatures are elevated for long periods.

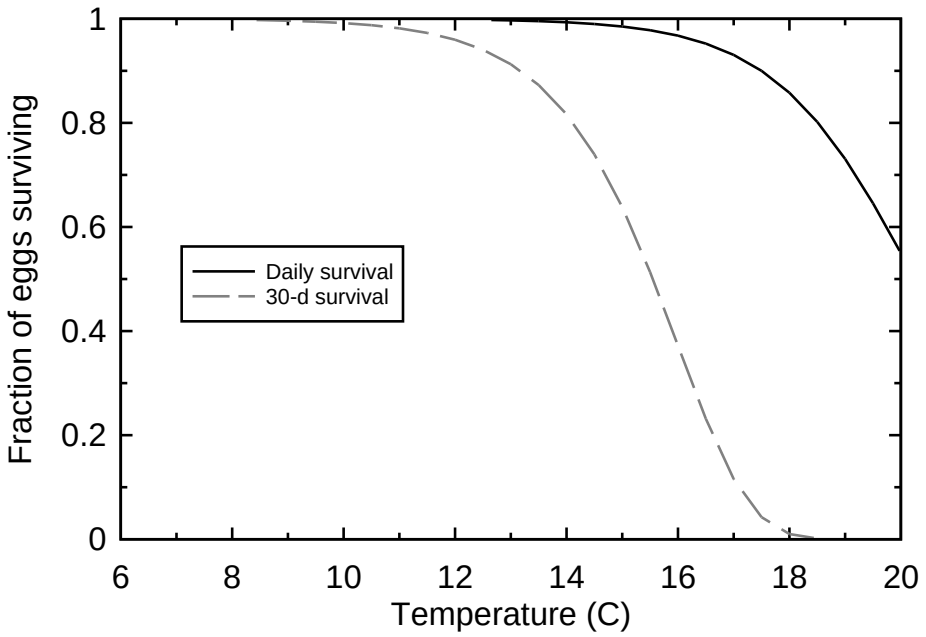

Figure 43. High temperature redd survival function, for Chinook salmon parameter values.

Table 19. Parameter values for high temperature redd mortality.

Parameter	Definition	Species	Value
mortReddHiTT1	Temperature at which high temperature survival of eggs is 10 pct (°C)	Chinook	23
mortReddHiTT9	Temperature at which high temperature survival is 90 pct (°C)	Chinook	17.5

8.1.5 Superimposition

Superimposition redd mortality can occur when a new redd is laid over an existing one; females digging new redds can disturb existing redds and cause egg mortality through mechanical damage or by displacing eggs from the redd environment. It is believed that superimposition typically causes mortality of many but not all eggs in a redd (Essington et al. 2000, Hendry et al. 2003). *inSALMO* assumes that superimposition is accidental with no bias for or against spawning over existing redds. The study by Essington et al. (1998) indicates that stream trout may indeed intentionally superimpose their redds over existing ones, a practice that has the advantages of reducing (a) the work necessary to clean redd gravels and (b) the competition that the spawner's offspring will face (Morbey and Ydenberg 2003). The formulation could be modified to represent intentional superimposition and the complex effects that it might have, but there is currently little known about what factors (e.g., sediment quality, spawner density) might encourage intentional superimposition.

Superimposition redd mortality is modeled as a function of the area disturbed in creating the new redd and the area of spawning gravel available. The following steps are executed by each redd, on each day it exists:

1. Determine if one or more new redds were created in the same cell on the current day. If not, then superimposition survival is 1.0 and the remaining steps are skipped.

2. In the event that *cellFracSpawn* is zero, there is no risk of superimposition and the remaining steps are skipped. This assumption is made because there is no gravel to be disturbed by another spawner.

3. If the female that created the redd is still alive, then the redd is assumed to be defended and superimposition survival is 1.0 and the remaining steps are skipped.

4. If one or more redds (of any species) were created in the same cell on the current day, the probability of them causing superimposition (*reddSuperImpRisk*, unitless) is equal to the total area of these new redds divided by the area of undefended spawning gravel in the redd.

$$reddSuperImpRisk = \frac{newReddsArea}{(cellArea \times cellFracSpawn) - defendedArea}$$

   The total area of new redds (*newReddsArea*) is the sum, over all redds created in the cell on the current day, of *reddSize*. The fish parameter *reddSize* (cm^2) is a characteristic area of the redd pit and tailspill, and is species-specific. The cell area defended by spawners (*defendedArea*) is the sum, over all live females who have already spawned (including those who spawned on the current day) of the fish parameter *fishSpawnDefenseArea*. This parameter represents the typical area (cm^2) that a female defends around her redd. If the denominator in the equation for *reddSuperImpRisk* is zero, or less than *newReddsArea* (so *reddSuperImpRisk* would be greater than one), then *reddSuperImpRisk* is set to 1.0.

5. A random number is drawn from a uniform distribution between zero and one; if it is less than *reddSuperImpRisk*, then superimposition mortality occurs.

6. If superimposition mortality occurs, then the fraction of eggs surviving is the value of another random number drawn from a uniform distribution between zero and one.

The parameter *reddSize* is defined as the area a spawner disturbs in creating a new redd. For Chinook salmon, a value of 56,000 cm^2 is supported by observations in the lower Columbia River basin (Burner 1951) and in Clear Creek, Sacramento River basin (Newton and Brown 2004). Burner (1951) noted that spawners tended to defend an area about four times the area of their redds, so a corresponding value of *fishSpawnDefenseArea* is 200,000 cm^2.

8.2 Development

To predict the timing of emergence, the developmental status of a redd's eggs is updated daily. Model redds accumulate the fractional development that occurs each day (*reddDailyDevel*), a function of temperature. This means the redd has a variable *fracDeveloped* that starts at zero when the redd is created and is increased each day by the value of daily value of *reddDailyDevel*.

When *fracDeveloped* reaches 1.0, then the eggs are ready to emerge. The daily value of *reddDailyDevel* is determined using the equation recommended by Beacham and Murray (1990; their Model 4):

$$reddDailyDevel = \frac{1}{reddDevelParamA \times \left(temperature - reddDevelParamC \right)^{reddDevelParamB}}$$

Parameter values for chinook salmon from Beacham and Murray (1990; Table A.3 for fry emergence) are: *reddDevelParamA* = 33,000; *reddDevelParamB* = -2.04; *reddDevelParamC* = -7.58. The effect of temperature on development time for these parameter values is illustrated in Figure 44.

(The analysis of Beacham and Murray 1990 also indicates that eggs hatch into alevins when redd development reaches 0.6.)

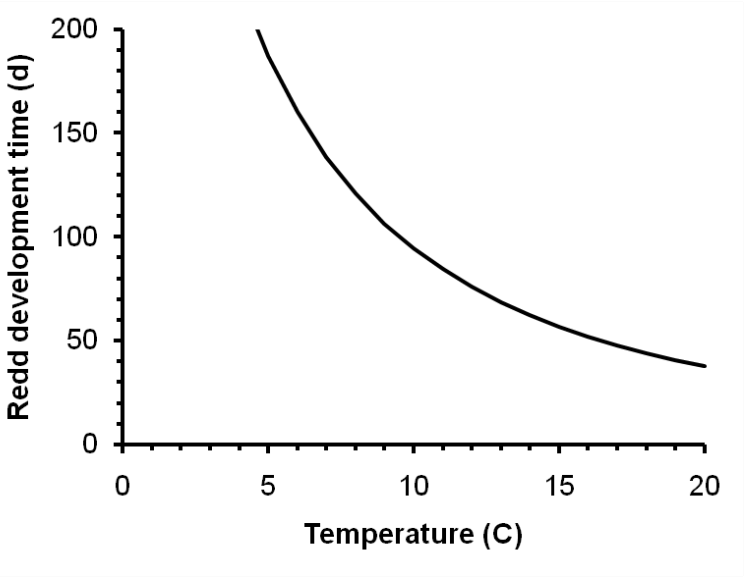

Figure 44. Redd development time (days from redd creation to emergence) vs. temperature for chinook salmon; the graph depicts the denominator of the equation for *reddDailyDevel*.

8.3 Emergence

"Emergence" is the conversion of each surviving egg into a new juvenile salmon object. When a redd's value of fracDeveloped equals or exceeds 1.0, its eggs are considered fully developed and ready to emerge as new fish. New fish emerge over several days. The following steps are used to determine how many fish emerge each day.

8.3.1 Emergence timing

Emergence begins on the day when *fracDeveloped* reaches 1.0, then the new fish emerge over a period of several days. Causing emergence to occur over several days reproduces observed natural variation in emergence timing and can potentially have strong effects on survival of newly emerged trout. These fish compete with each other for food as soon as they emerge. If all

emerged on the same day, without time for some to move, competition would probably be overestimated. As a simple way to spread emergence over several days, *inSALMO* assumes that 10% of the redd's eggs emerge on the first day of emergence; 20% of the redd's remaining eggs emerge on the next day; 30% of the remaining eggs emerge on the third day; etc, until 100% of remaining eggs emerge on the 10^{th} day. For example, if a redd contains 100 eggs on the day that development is complete, 10 new trout will be created on that day and 90 eggs will remain. On the next day (assuming no egg mortality occurs), 18 new fish will be created (20% of 90) and 72 eggs (90-18) remain in the redd. On the third day of emergence, 21 eggs (30% of 72, truncated to an integer) emerge. As emergence proceeds, the eggs remaining in a redd remain susceptible to egg mortality.

8.3.2 New fish attributes

For each new fish created from an egg that emerges, the model assigns these attributes.

- The fish is assigned its species from that of the redd.
- The fish is placed in the same habitat cell as its redd.
- Sex is assigned randomly, with even probability of being male or female.
- The length of each individual fish (*fishLength*, cm) is assigned from a uniform random distribution with minimum length equal to the fish parameter *reddNewLengthMin* (cm) and maximum length equal to the parameter *reddNewLengthMax* (cm).
- Weight (*fishWeight*, g) is calculated from length, using the length-weight relationship and parameters used in modeling growth (Section 7.3.1) and to create initial fish (Section 9.2). Fish are assumed to have a normal condition factor (*fishCondition* = 1.0) when they emerge:

$$fishWeight = fishWeightParamA \times fishLength^{fishWeightParamB}.$$

Variation among individuals in length at emergence is represented because habitat selection (and, consequently, growth and survival) is modeled using a length-based hierarchy (Section 7.2.1). Elliott (1994) found fish emerging from a redd to vary in size only slightly; but the variation gives larger fish an advantage in dominance that is likely to persist and grow over time because competition among newly emerged fish is often intense.

Example length parameter values for newly emerged Chinook salmon are provided in Table 20. These values were estimated from unpublished data provided by Michael Sparkman (California Department of Fish & Game, Arcata, CA) from four emergence traps deployed in the Redwood Creek drainage, Humboldt County, 1996-99.

Table 20. Parameter values for size of newly emerged fish.

Parameter	Definition	Chinook salmon value
reddNewLengthMin	Minimum of uniform distribution from which new fish lengths are drawn (cm)	3.5
reddNewLengthMax	Maximum of uniform distribution from which new fish lengths are drawn (cm)	4.1

8.3.3 Superindividual subadults

When juvenile salmon are created upon emergence from redds, they optionally can be modeled as "superindividuals" to reduce computations and significantly reduce the time that *inSALMO* takes to execute. Superindividuals are model objects that behave exactly as a normal fish but represent multiple individuals. Each fish in *inSALMO* has an instance variable *nREP*, an integer for how many fish are represented by it. Adults are initialized with *nREP* set to 1 so they always represent just one fish.

When juveniles are created upon emergence from their redd, their value of nREP is set equal to a model variable *juvenileSuperindividualRatio*, which is given a value in the Model.Setup file. If, for example, *juvenileSuperindividualRatio* is set to 10 in Model.Setup, then the number of new fish created from a redd is about $1/10^{th}$ the number of eggs that hatch, and each such fish represents 10 real fish. The following methods are used.

- On days when its is fully developed, a redd calculates how many eggs emerge as new fish (Section 8.3.1).

- If this number of emerging eggs is less than the value of *juvenileSuperindividualRatio*, then one new fish object is created with its value of *nREP* set to the value of *juvenileSuperindividualRatio*. The redd is then assumed to be empty.

- If instead the number of emerging eggs is greater than the value of *juvenileSuperindividualRatio*, then the number of new fish objects created is calculated by dividing the number of emerging eggs by *juvenileSuperindividualRatio* and rounding the result to an integer. This number of new fish objects are created and their value of *nREP* set to the value of *juvenileSuperindividualRatio*. The number of eggs remaining in the redd is set by subtracting the number of emerging eggs (not the number of new fish objects times *juvenileSuperindividualRatio*) from it.

- During its habitat selection method, a fish compares the available drift and search food in potential destination cells to the food it would consume in the current day. In this method the food the fish would consume is multiplied by its value of *nREP* to account for the multiple fish it represents.

- When a fish occupies a cell and feeds there, the food and velocity shelter it consumes is multiplied by *nREP*.

- The file output for number of live and dead fish are modified so instead of reporting the count of fish objects they report the sum of *nREP* over the fish. These outputs therefore report the number of represented fish, not the number of fish objects. (However, the graphical outputs, including the animation raster and the graphs, report the number of fish objects, not multiplied by *nREP*.) File output for biomass are likewise adjusted for *nREP* so they report the total mass of fish represented (biomass output sums the product of individual weight and *nREP* over all fish objects).

It is important to understand the effects of superindividuals on model results: this technique can introduce biases that are difficult to predict. To understand how superindividuals affect results, an experiment ran inSALMO for *juvenileSuperindividualRatio* values of 1, 5, 10, 20, 50, and 100; with 50 replicate simulations of each value. The model was run for one year using two study sites. Results indicate that values of *juvenileSuperindividualRatio* above 20 can have relatively strong effects on abundance, especially at the end of the season when juvenile numbers become low (Figure 45). Likewise, high values of *juvenileSuperindividualRatio* can have strong effects on juvenile lengths during periods when abundance is low (Figure 46).

An experiment with a simple test program, in which superindividuals do nothing but survive daily with probability of 0.99, produced an increase in mean abundance with increasing superindividual ratio similar to that in Figure 45. This experiment indicates that the effect of superindividual ratio is largely an artifact of the survival mathematics. The effect of *juvenileSuperindividualRatio* on length likely results from changes in abundance, which affect competition for feeding sites.

Length of the few fish that migrate out latest can be a very important outcome of *inSALMO*, so artifacts of *juvenileSuperindividualRatio* should be carefully avoided. Values above 20 appear risky, while values of 10 and lower had little apparent effect in this experiment.

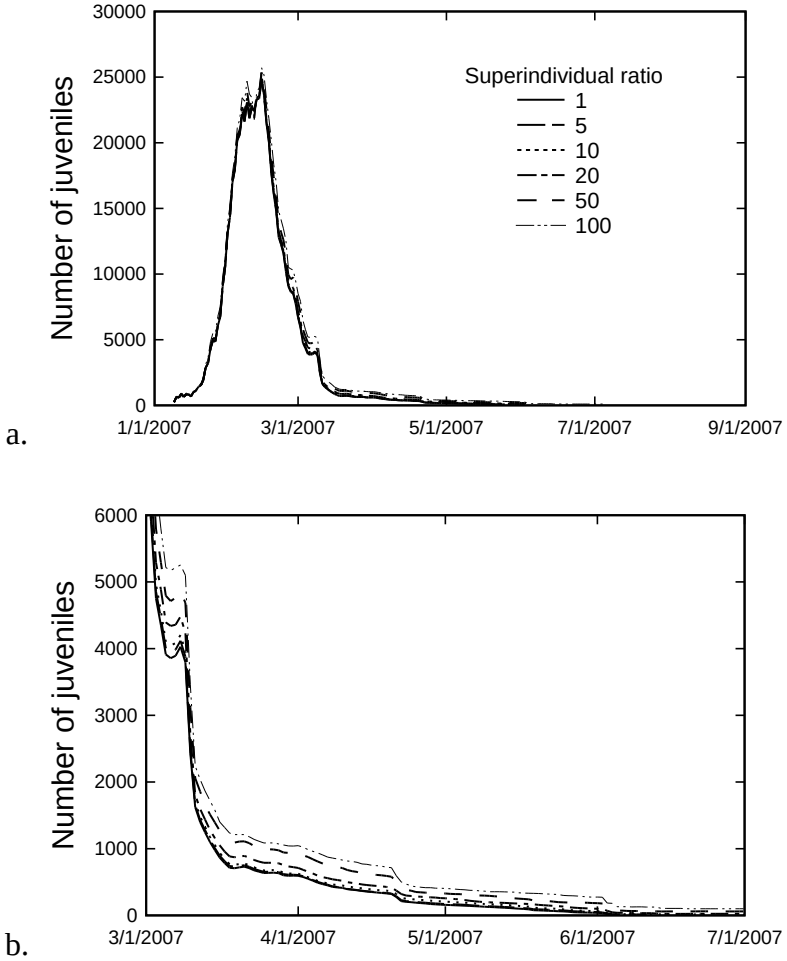

Figure 45. Effect of *juvenileSuperindividualRatio* on juvenile abundance. Results are means of 50 replicates. Panel b is simply a zoom in on March 1 to July 1 results.

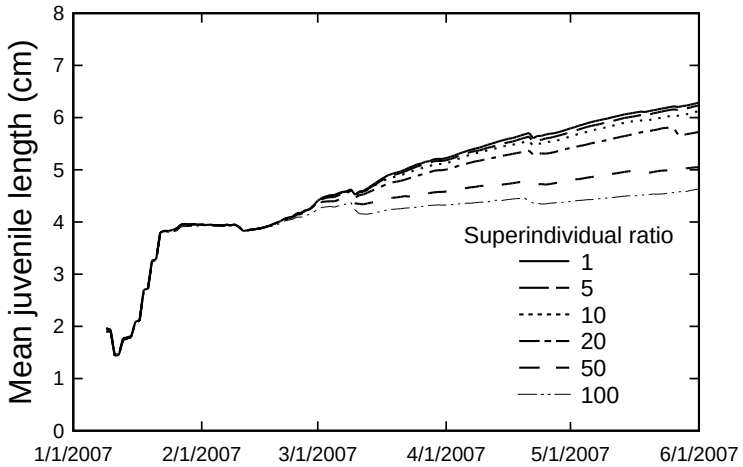

Figure 46. Effect of *juvenileSuperindividualRatio* on juvenile mean length. Results are means of 50 replicates.

8.4 Empty Redds

As described in the previous sections, the number of eggs remaining in redds is reduced when eggs die or fish emerge. When the number of remaining eggs in a redd reaches zero, the redd is dropped from the model.

9 inSALMO Model Description: Initialization

This section describes the methods used to initialize the habitat and fish populations when each new model run is started. Because *inSALMO* 1.0 is designed to simulate one or more seaasons of spawning through outmigration, the start of a simulation is typically just before adults arrive via migration from the ocean, with no salmon present. Although this section mentions some of the input types and files, complete documentation of file and input types is provided in a separate software document.

9.1 Habitat Initialization

A model run starts by reading in the habitat characteristics that do not change during the simulation. These characteristics are the number of reaches and how they are linked, the location and dimensions of cells in each reach, the values of cell variables that do not change with time, and the lookup tables used to calculate daily depth and velocity in each cell (Section 6.2). Finally, variables that depend on time-series input (reach temperature, flow, turbidity; cell depth and velocity) are initialized with the input data for the first simulation date.

9.2 Fish Initialization

At the start of a simulation, *inSALMO* creates the adult spawners that then "arrive"—are added to the model at their designated reach—over time as the simulation proceeds. These adults are the only salmon initialized.

9.2.1 Spawner arrival dates

The number of adults and their initial characteristics are specified as model input, via a population initialization file. These initial characteristics include the date at which each adult "arrives" and enters the simulation. The method for distributing spawner arrival dates is taken from *inSALMO* 0.5, which assumes a truncated normal distribution. The parameters for the distribution of arrival dates are provided as part of the population initialization input for each species, reach, and year. The initialization input variables *arrivalStartDate* and *arrivalEndDate* (in MM/DD/YYYY format) specify the first and last dates of arrival. The peak date of arrival is by definition halfway between these first and last dates. The variable *arrivalRatio* specifies the ratio of the distribution's peak height (at the middle of the arrival period) to the distribution's height on the first and last arrival days (Figure 47). The algorithm to assign arrival dates to spawners is:

- The first and last arrival dates are set to *arrivalStartDate* and *arrivalEndDate*.
- The mean (peak) arrival date is set equal to the mean of *arrivalStartDate* and *arrivalEndDate*.
- The standard deviation in arrival dates is set to the length of the arrival period (difference between last and first days) divided by $2[-2\ln(arrivalRatio)]^{0.5}$.

- For each spawner initialized, a random value is drawn from a normal distribution with the above mean and standard deviation, then rounded to an integer date. If this date is before the first arrival date or after the last, it is discarded and another value drawn.

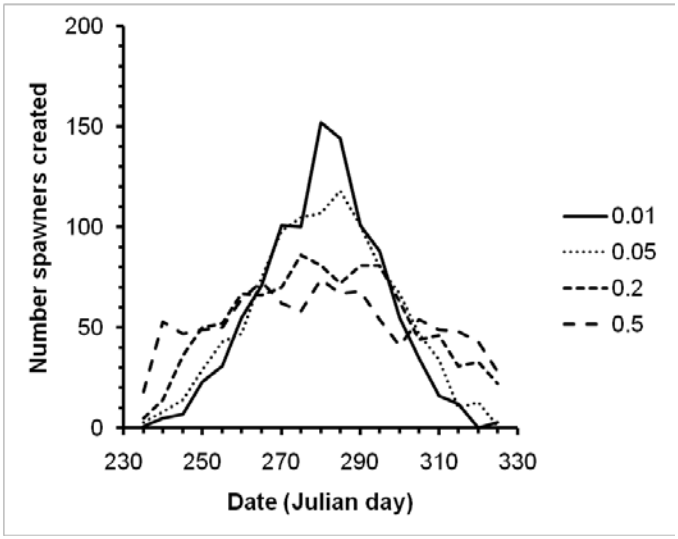

Figure 47. Example distributions of spawner arrivals (number of arrivals in 5-day periods, out of 1000 total adults) for four values of *fishArrivalRatio* (0.01–0.5), with *fishArrivalStartDate* and *fishArrivalEndDate* set to 8/26/2005 (Julian day 238) and 11/25/2005 (Julian day 329).

9.2.2 Initialization of spawner numbers, locations, and variables

The number and sex distribution of initial spawners is specified by input. Separate input values for each species, year, and reach specify the number of spawners to create and what fraction of them are female. If, for example, 200 spawners are to be created for a reach and the fraction female is 0.6, then exactly 120 females and 80 males are created.

Spawner lengths are drawn randomly from a normal distribution with mean and standard deviation specified as input (also for each species, year, and reach). Because length can differ between males and females and only the female's length matters to the model (because it determines fecundity), these spawner length parameters should represent females only. The weight of each fish is calculated from its length using parameters *fishWeightParamA* and *fishWeightParamB* and the method used for new juveniles (Section 8.3.2).

In this version of *inSALMO*, spawner ages do not need to be simulated. Instead of removing the age variable (it may be needed in subsequent versions of the model) or specifying it in input (making the input more complex), the age of every spawner is simply set to 5 years.

When adults are added to the model on their arrival date, they are placed in a cell chosen randomly from among those having depth greater than one tenth of the spawner's length. (A cell is chosen randomly then tested for whether it meets the depth criterion. Up to 10,000 cells are tried; if none meet the criterion, then the model stops.)[7]

[7] The cell choice process is revised in v. 1.5.

Fish have two variables controlling when and if they spawn. The variable *isSpawner* is initialized to YES, indicating that all adults are eligible to spawn during the current spawning season. The variable *spawnedThisSeason* indicates whether the fish has already spawned during the current spawning season (Section 7.1.1) and is initialized to NO.

9.3 Redd Initialization

There is no capability in *inSALMO* to initialize redds at the start of a simulation. Redds can only be created by spawning fish.

10 inSALMO Model Description: Random Number Generation

Several processes in *inSALMO* (e.g., fish initialization; fish survival) are modeled stochastically, using pseudo-random numbers to determine process outcomes. How pseudo-random numbers are generated is an important issue for any stochastic simulation model, as poor quality or mis-used random number generators can bias simulation results.

All pseudo-random numbers in *inSALMO* are generated by the MT19937 "Mersenne Twister" algorithm, the default generator in the Swarm software platform used to implement *inSALMO*. (See SDG 2000 for additional information and references.)

One random number generator is used for all stochastic processes in *inSALMO*. This generator is initialized with a random number seed, *randGenSeed*, provided by the user as a model parameter. If two model runs use the same value of *randGenSeed* and exactly the same input and parameters, the two runs will produce exactly the same results. However, any change to input (parameter values, input data, simulation dates, etc.) is very likely to alter the number of times the random number generator is called and, therefore, the outcome of all stochastic processes. Replicate simulations are produced by altering only the value of *randGenSeed*.

11 inSALMO Model Description: Scheduling

The order in which events occur can strongly affect the outcome of individual-based models. This section defines the schedule by which the events in *inSALMO* are executed. The schedule consists of an ordered list of actions, each executed once per simulation day. An action is defined by a list of objects, the methods those objects execute, and rules for the order in which the objects are processed. There are four main action groups (groups of related actions over the same list of objects): habitat, fish, redd, and observer. The full schedule is displayed at the end of this section.

11.1 Spawner Arrival

Any spawners scheduled to "arrive" from the ocean on the current day (Section 9.2) are inserted into their reach.

11.2 Habitat Update Actions

Habitat updates are scheduled first because subsequent fish and redd actions depend on the day's habitat conditions. For each reach, time-series input data (flow, temperature, turbidity) are obtained for the current simulation date. The new flow is used to update the depth and velocity of all cells in each reach. The daily food production is calculated for each cell, and the amount consumed by fish is reset to zero.

11.3 Fish Actions

Fish actions are scheduled before redd actions because one fish action (spawning) can cause redd mortality via superimposition. This order means that new fish emerging from a redd do not execute their first fish actions until the day after their emergence. Scheduling fish spawning before redd actions also means that redds undergo all redd actions on the day they are created.

The four fish actions in the model are conducted in the following order: spawning, habitat selection, growth, and survival. Actions are carried out one fish at a time, in descending order of fish length. Each of these four actions is conducted for all fish before the next action is executed.

Spawning is the first fish action because spawning can be assumed the primary activity of a fish on the day it spawns. Spawning also affects habitat selection in two ways. First, female spawners move to a cell with spawning habitat on the day they create a redd. Second, when fish spawn their weight and condition are substantially reduced, which affects their choice of habitat (giving higher preference to habitat providing high growth).

Habitat selection is the second fish action each day because it is the way that fish adapt to the day's new habitat conditions; habitat selection strongly affects both growth and survival. Note that habitat selection is affected by fish size and condition (which affect survival probabilities and reproductive status). Habitat selection is based the fish's size *before* the current day's growth, because a fish's growth depends on its habitat choice.

Growth is scheduled before survival because changes in a fish's length or condition factor affect its probability of survival.

The last fish action is survival. Survival has its own sub-schedule because it includes evaluation of several different mortality sources. The number of fish killed by each mortality source can be affected by the order in which survival probabilities for each source are evaluated. Placing a mortality source earlier in the survival sub-schedule makes it slightly more likely to cause mortality (a mortality source cannot kill a given fish on a given day if a preceding mortality source kills the fish first). Therefore, widespread, less random mortality sources (e.g., high temperatures, high velocities) are scheduled first; survival probabilities for these sources tend to be negligible (very close to 1.0) under most conditions and low (causing high mortality) when an unusual event occurs.

11.4 Redd Actions

Redd actions occur last each day because redds do not affect either habitat cells or fish (with the exception of creating new fish, as discussed above). There are three redd actions: survival, development, and emergence. These actions are applied to the existing redds in the order in which the redds were created, but this order has no effect on redds or newly emerged trout.

Redd survival is the first redd action to be executed. Survival is scheduled before emergence so that eggs are subject to mortality on the day they emerge; otherwise, emerging fish would risk neither redd mortality nor fish mortality for one lucky day. Redd survival includes five separate egg mortality sources which follow their own sub-schedule. The redd mortality sources are scheduled from least random (extreme temperatures) to most random (superimposition).

Development is the second redd action, and emergence is third. Because development preceeds emergence, new fish begin to emerge from a redd on the same day the redd's egg development is complete.

11.5 Observer Actions

Observer actions collect and record data on the digital world inside *inSALMO*. Because the output produced by observer actions is the only information that users have about the complex events going on inside the model, fully understanding model results requires knowing how observations are scheduled with respect to other model actions.

Observer actions are the last of the daily model actions. Therefore, the model's graphical and file outputs represent the state of the model after all the habitat, fish, and redd actions have been completed for a day. This scheduling means, for example, that the size and condition of a fish observed from the graphical user interface reflects the fish's state after it has completed its daily feeding and growth, not its state when it made its habitat selection decision or when it considered spawning.

11.6 Complete Schedule

The complete schedule is displayed in Figure 48. This figure displays the four main action groups and the actions within each group, in the order they are executed on each daily time step.

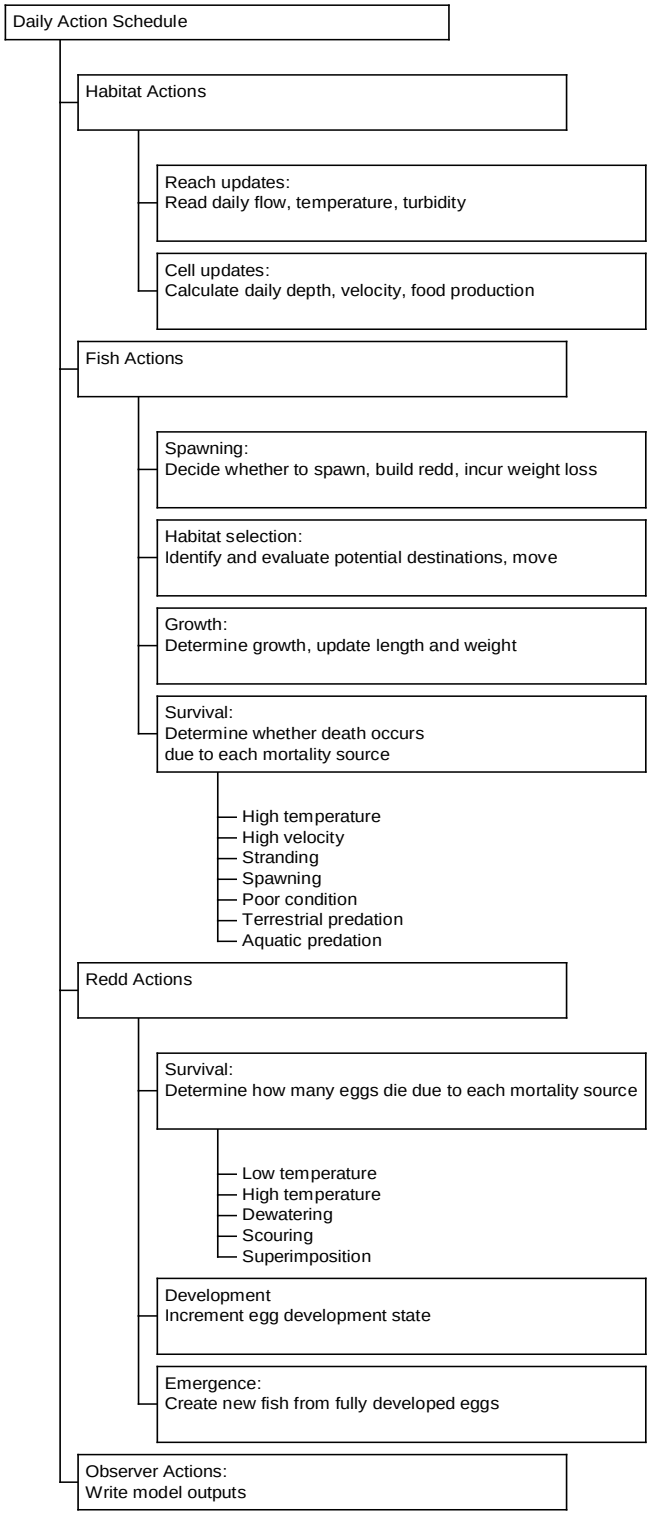

Figure 48. Complete schedule of daily actions.

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