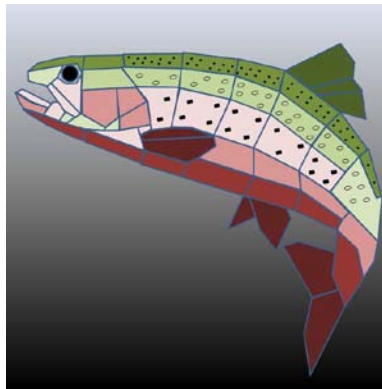# *inSTREAM-SD*:
The Individual-based Stream Trout Research and Environmental Assessment Model
with Sub-Daily Time Step, Version 6.1
Model Description

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Change log:

Date	Change
12 December 2013	Original publication of inSTREAM 6.
8 August 2014	Clarify that condition is updated immediately at spawning (Sect. 5.1.5).
8 August 2014	Change method for calculating length resulting from a change in weight (Sect. 5.3.1). This change increases execution speed but is exactly equivalent to the previous method.
13 November 2014	Add changes in drift concentration as potential triggers for time steps (Sect. 4.1.3).
16 December 2014	Revise spawning site selection so spawner considers suitability over a 24-hour period (Sect. 5.1).

Increment version number to 6.1. |
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Contents

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1 Introduction, Objectives, and Background

1.1 Document Purpose and Overview

This document describes version 6.1 of *inSTREAM*, the *in*dividual-based *S*tream *T*rout *R*esearch and *A*ssessment *M*odel; this version is also known as *inSTREAM-SD* because it represents sub-daily time steps. (Version 6.0 was distributed prior to December, 2014; the transition to version 6.1 was made with changes to Sect. 5.1.2 making spawners select habitat cells that have been suitable over a full day's flows.)

This document is modified from a series of documents describing previous versions of *inSTREAM*. These include the USDA Forest Service report (Railsback et al. 2009) that provides complete documentation of version 4.2 of *inSTREAM*, and a report prepared for Argonne National Laboratory and the Electric Power Research Institute describing version 3, the previous version of *inSTREAM-SD* (Railsback et al. 2006).

This document uses the same section numbering as Railsback et al. (2009), so the same topics are covered in the same major sections of both documents, through Section 12.

Users and potential users of *inSTREAM-SD* are encouraged to periodically check the web site for individual-based ecological modeling at Humboldt State University: http://www.humboldt.edu/ecomodel. Improvements and fixes to *inSTREAM*, its software, and this documentation are likely and will be posted on this site.

1.2 Summary of changes from version 3

Version 6 is a major revision of *inSTREAM-SD* because of changes in how habitat is depicted and because of substantial changes in software. There are few changes in how fish are modeled. The major changes from version 3 are:

1. Habitat is represented as multiple, linked reaches with fish moving among reaches.

2. The habitat model is independent of hydraulic models. Version 3 used output files from a specific two-dimensional hydrodynamic model as input representing cell geometry and hydraulics (depth and velocity). Now, both the geometry and hydraulics are input to *inSTREAM* in generic formats and can be prepared via geographic information systems (GIS) from output of any hydraulic model.

3. The trout model is packaged with a graphical user interface (GUI) that simplifies and automates many common tasks. The GUI identifies many kinds of mistake in input files, assists in setting up simulation experiments, provides an automated "limiting factors" analysis for comparing the importance of a number of habitat variables, and imports key results to an Excel spreadsheet that provides summary statistics and graphics. The GUI also provides help files including the model description, a software guide, and user guides to the limiting factors tool and to the GUI itself.

4. Input and output file formats have been modified to work more easily with spreadsheet and statistical software.

5. The model and GUI execute as Windows-native executables, so Windows users need not install and learn to use the Cygwin Unix emulator that previous versions required. (Code is still provided to run *inSTREAM*, but not the GUI, in Linux systems that have Swarm installed. Sixty-four-bit execution, which can be considerably faster, is available only in Linux.)

1.3 Citing the model and this document

Please cite the *inSTREAM* 6.1 model, including this document and the model software, as:

Railsback, S. F., B. C. Harvey, and C. Sheppard. 2014. *inSTREAM-SD*: The Individual-based Stream Trout Research and Environmental Assessment Model with Sub-Daily Time Step, Version 6.1. www.humboldt.edu/ecomodel.

Railsback et al. (2006) can also be cited as a description of the model, with the exception of the changes listed above.

1.4 Acknowledgements

2 Overview of *inSTREAM-SD*

2.1 Fundamental Assumptions

The first step in understanding and using *inSTREAM-SD* is to understand its fundamental assumptions. These assumptions are presented using the conceptual framework for IBMs suggested by Railsback (2001) and Grimm and Railsback (2005).

Emergence. The most fundamental assumption of IBMs such as *inSTREAM* is that population and community responses <u>emerge</u> from processes acting at the individual level. In *inSTREAM*, trout population and community responses include many characteristics of real fish communities: abundance and relative abundance of trout species; biomass; production; statistical distributions of age, weight, and length; habitat use patterns; and measures of persistence such as mean time to extinction. These population characteristics emerge from the growth, survival, and reproduction of individuals, while these individual-level processes are affected by habitat inputs such as flow, temperature, turbidity, and channel shape.

Adaptation. How population responses emerge from individual growth, survival, and reproduction is strongly determined by how the individuals adapt to changes in themselves and their habitat. In *inSTREAM-SD*, the primary adaptive traits used by trout are <u>habitat</u> <u>selection</u> and <u>activity selection</u>. Habitat selection is the decision of which habitat cell to occupy each time step. Activity selection is the choice each time step between two activities: feeding or hiding.

Other adaptive traits are selecting which of two feeding strategies a fish uses each day; and the decision by adult females of when and in which cell to spawn.

Trout have many adaptive behaviors that we have chosen <u>not</u> to represent mechanistically in *inSTREAM-SD*, because doing so does not seem necessary to meet the model's purposes. These include deciding whether to allocate energy intake to growth, energy storage, or gonad production; and deciding whether to spawn each year.

Fitness. The habitat and activity selection traits are modeled as a fitness-seeking process in which trout select the activity and cell that offers the highest value of a measure of expected fitness. The fitness measure used in *inSTREAM* is the "Expected Reproductive Maturity" measure developed by Railsback et al. (1999) and tested by Railsback and Harvey (2002).

Interaction. Trout interact with each other via indirect competition for food, feeding habitat (velocity shelters), and hiding habitat. (The term "exploitation competition" is also used in ecology for this kind of interaction.) Competition follows a length-based hierarchy. Each habitat cell contains a limited daily food supply and a fixed area of velocity shelter and hiding habitat. Food consumption by larger individuals potentially limits the amount of food a trout could get if it occupied the same cell. Each trout is assumed to consume the lesser of two amounts: (1) the amount of food it can catch in a day, and (2) the amount available: the cell's daily food supply minus the amount consumed by all the larger trout in the cell. A similar approach is used to allocate velocity shelter area and hiding habitat.

Stochasticity. *inSTREAM-SD* is not a highly stochastic model. The most important stochastic process mortality. The <u>probability</u> <u>of</u> <u>survival</u> for each trout is a deterministic function of its state and its habitat; but whether the trout actually lives or dies each time step is a stochastic event. The other use of stochasticity is initializing a model run: input files specify how many trout of each age are to be initialized, and the mean and standard deviation of length for each age class. The actual length of each individual is drawn from a random distribution with the specified mean and standard deviation; its sex is assigned randomly; and the individual's initial location is selected randomly from the cells with non-extreme depths and velocities. A similar approach is used to assign the length of new fish produced in the model as they hatch from eggs. Another stochastic process determines whether a female that is ready to spawn actually does spawn on a particular day. Some of the methods for representing mortality of incubating eggs are also partially random. The model incorporates environmental variability through the driving physical variables: stream discharge, turbidity, and temperature.

Spatial scales. Space is represented at three scales. The entire simulated space is one or more reaches, and each reach is a collection of polygonal cells. Cells can be either irregular or rectangular, depending on what kind of hydraulic model is used (Figure 1). Habitat conditions can vary among cells but not within a cell. The spatial resolution is therefore the size of one cell. Cell dimensions are chosen in the field to best represent the actual habitat, but recommended cell sizes are greater than the area typically occupied by one adult trout (very roughly, 1 m^2). Some habitat variables (temperature, turbidity) vary among reaches but not among the cells within each reach. The spatial extent (the total area simulated) is chosen by the user as a tradeoff between representing the study site (better with larger areas) and the field data and computational effort needed to represent larger areas. The spatial extent of *inSTREAM* can include multiple, linked stream reaches. 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.
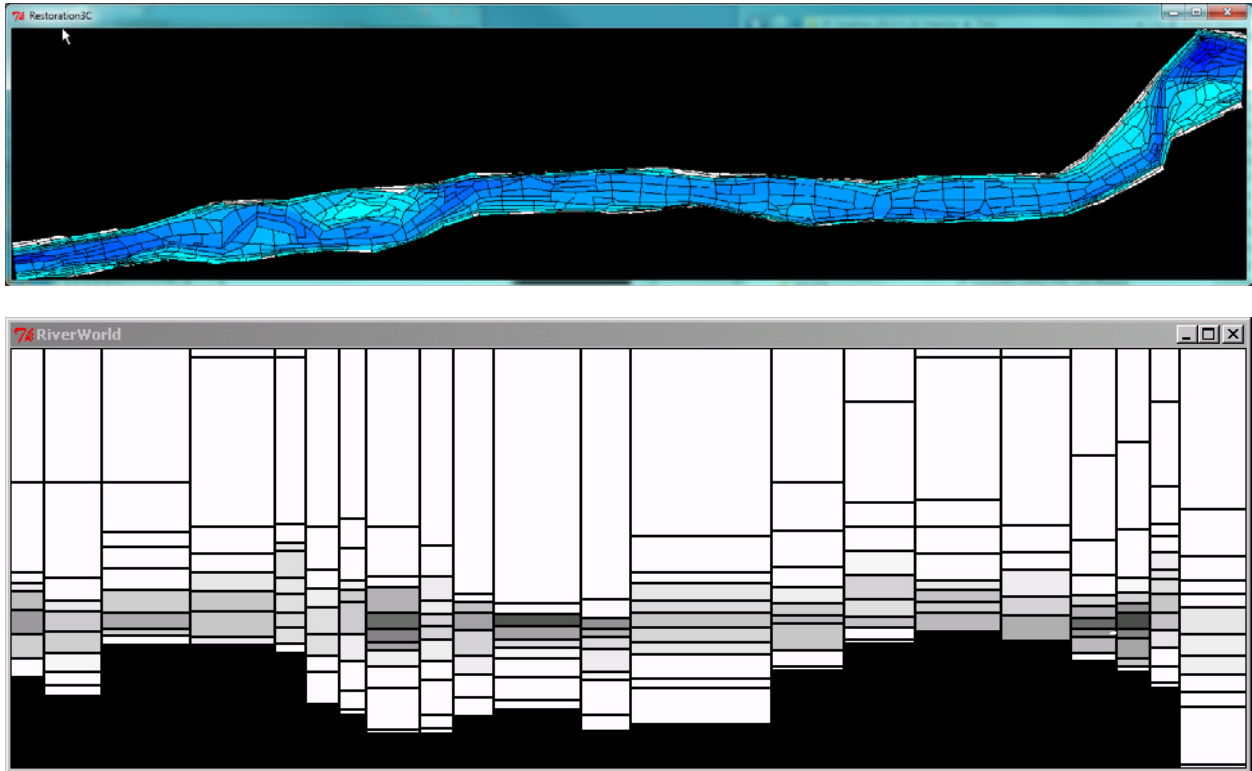
Figure 1. Representations of space in *inSTREAM* 6. Top: polygonal cells generated in a geographic information system (GIS) or two-dimensional hydrodynamic model. Bottom: rectangular cells from a pseudo-two-dimensional hydraulic model. These are each a plan (top-down) view of one reach.

Scheduling and temporal scales. Time is modeled using discrete time steps. *inSTREAM-SD* uses a flexible time step, with a minimum of two and maximum of 24 steps per day. Time steps are chosen to allow fish to adapt their habitat and activity to changes in daylight and in flow. Time steps are therefore triggered by the transitions between daytime and night and by changes in flow from hour to hour that exceed a user-selected threshold. The schedule of model actions within each time step is summarized in Section 2.2. Users select the temporal extent (duration) of model runs; five to 10 year runs are typical.

Habitat input variables. There are four time-varying inputs to *inSTREAM-SD*: As in previous versions of *inSTREAM*, values of temperature and turbidity are input for each day. Because it is designed to simulate effects of within-day flow changes, *inSTREAM-SD* uses hourly input for flow (m^3/s of water through the reach). To allow simulation of temporal variation in food availability, *inSTREAM-SD* treats the concentration of drift food (g/cm^3) as an hourly input variable. Users can therefore model drift concentration as a function of temperature, flow, etc., at hourly and longer time scales and input the resulting drift scenarios. These four variables are assumed uniform throughout a reach but can vary among reaches.

There are also habitat inputs that are constant over time but variable among cells; these variables define the size and location of cells and the availability of habitat resources such as hiding and feeding cover and spawning gravel. Each cell also has hydraulic parameters that determine the cell's daily depth and water velocity from the reach's flow rate. A variable for the availability of search food (Section 4.2.4) is assumed constant over both space and time. Habitat input also defines how multiple reaches are linked together.

4

Stocking of hatchery fish is simulated in *inSTREAM-SD*. Input specifies the date, number, and characteristics (species, length distribution) of each stocking event.

Outputs. Unlike conventional population models, *inSTREAM* produces a variety of output types. One type is summary statistics of population status: abundance; mean, minimum, and maximum length; mean weight; etc., broken out by species and age class. Statistics on habitat use (e.g., histograms of fish abundance vs. velocity) are also produced. Another type of output is mortality data: how many fish and eggs died due to what causes. Optional graphical output displays the location and size of individual fish so patterns of habitat use and movement behavior can be observed.

2.2 Trout Species and Number of Species

Through some simple software edits explained in the software guide, *inSTREAM* can be made to represent any trout species and any number of species. Most model outputs are reported separately for each species, and each species has its own set of parameter values. (Its object-oriented software also makes it easy to modify *inSTREAM* so that different species use different methods for selected processes.) Trout are assumed not to mate with members of another species (Section 5.1). Model trout are not separated by species within the software, and the order in which trout are processed each step is determined only by their length, not species.

2.3 Summary of Model Actions and Schedule

This subsection provides a summary of the objects in *inSTREAM-SD* and the actions they conduct. It also serves the very important purpose of defining the exact order in which model events are executed; the order in which events occur can strongly affect the outcome of individual-based models.

The model's schedule consists of an ordered list of actions, executed repeatedly. 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. The schedule for *inSTREAM-SD* is more complex than those of *inSTREAM* versions that operate at a strict one-day time step. Some actions are executed hourly, some at each model step, and some once per day or only on a few days. The full schedule is illustrated at the end of this subsection.

The schedule is based on several basic concepts:

- Actions that are not strongly affected by within-day flow changes (e.g., spawning, stocking, redd survival) are executed once per day.

- Actions that are affected by flow changes or phase (whether it is day or night) are executed at each model step, with a step being executed at change of phase and each flow change (Section 4.1.3).

- At each model step, the first actions executed are those that determine what happened (which fish died; how much fish grew) during the time step that just ended.

- The second actions executed at a model step are to produce output on the model's state at the end of the time step.

- The last actions executed at a model step are to update habitat and let fish adapt their behavior for the upcoming time step.

The complete schedule of *inSTREAM-SD* is described in the following list of actions. The list identifies the model objects that execute each action, when the action is executed, and what the action is. The model goes through this list each simulated hour to determine which should be executed. Fish actions are executed in descending length order (longest trout to shortest). Actions by reaches, habitat cells, and redds are executed in arbitrary order because order does not affect results.

1) Model:

   a) Update simulation time, day/night phase

2) Reaches:

   a) Input hourly flow

   b) If time = 00 h, input daily temperature and turbidity

3) Fish (if date = 1 January and time = 00 h):

   a) Increment age by 1 year

4) Reaches (if time = 00 h):

   a) Update maximum fish lengths (Section 5.2.5.2)

5) Model (if time = 10 h on a day when stocking occurs):

   a) Stocking (Section 8)

6) Fish (if time = first daytime hour):

   a) Spawn (Section 5.1)

7) Redds (if time = first daytime hour):

   a) Survive (Section 6.1)

      i) Dewatering

      ii) Scouring

      iii) Low temperature

      iv) High temperature

      v) Superimposition

   b) Develop (Section 6.2)

   c) Emerge (Section 6.3)

8) Model:

a) Determine whether a "step" occurs (a new time step begins, due to change in flow or day/night phase; Section 4.1.3)

9) Fish (if step occurs this hour):

   a) Survive (Section 5.4)

      i) High temperature

      ii) High velocity

      iii) Stranding

      iv) Aquatic predation

      v) Terrestrial predation

      vi) Poor condition

      vii) Angling

      viii) Hooking

   b) Grow (Section 5.3)

10) Model (if step occurs this hour):

   a) Report output for ending time step

11) Fish (if step occurs this hour):

   a) Select habitat and activity (Section 5.2)

3 Terminology and Conventions

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

3.1 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.

Activity. In *inSTREAM-SD*, fish choose between two activities: feeding and hiding.

Activity selection. The behavior and corresponding trait for selecting which activity to use in each model step.

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.

Calibration. The process of estimating the values of a few **parameters** to make the model reproduce field observations. While calibration is the primary means of evaluating parameters for simple models, for *inSTREAM* it is best to evaluate as many parameters as possible from the literature and, subsequently, calibrate only a few (see Section 17 of Railsback et al. 2009).

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

Data. Input that describes the habitat and fish population to be simulated. Data for *inSTREAM* Version 6 includes time series of flow, temperature, turbidity, and drift food concentration; cell dimensions and state variables; the relations between flow and depth and velocity for each cell; characteristics of the initial fish population; and characteristics of stocking events.

Fish, trout. The simulated fish individuals. Except where explicitly noted otherwise, these terms refer to virtual, not real, fish. Likewise, the words "egg" and "redd" refer to their virtual representation within *inSTREAM*.

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

Input. Any of the **data** and **parameter** values that a user provides to *inSTREAM* 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.

Model. This word is used in two ways. It sometimes refers to *inSTREAM-SD* in its entirety (e.g., "the model represents trout communities..."). However, it also sometimes refers to one object with specific actions (e.g., in Sect. 2.3). This "model" object is the part of *inSTREAM* that executes top-level actions such as keeping track of the date and time, and writing output files.

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 (as discussed throughout Section 5) or field data. A few parameters are best evaluated via **calibration** (discussed in Section 17 of Railsback et al. 2009).

Phase, day phase. Day or night.

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

Reach. *inSTREAM* models the trout population 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 *inSTREAM*, 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.

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); example system states are population biomass, number of species, and mortality rate (number of individuals dying per time step).

Step (or "model step"; contrast with "Time step"). We use the term "step" to represent a specific model action (Section 4.1.3) that ends one **time step** and begins the next. A step can be considered a jump in the simulated clock, at which events of the previous time step are completed and events at the start of the next time step are conducted.

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

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.

Time step. A simulated period of time; in *inSTREAM-SD*, each time step represents one to several hours.

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.

3.2 Conventions

3.2.1 Measurement units

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

Distance and length is 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, location, and characteristics 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). 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.

3.2.2 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:

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

and the corresponding program statement in the software is:

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

3.2.3 Survival probabilities and mortality sources

A number of factors can cause fish or fish eggs to die in *inSTREAM*. 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*.

3.2.4 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. (Users should be aware of the "Year 2038 problem" that will cause errors in 32-bit software, including the Windows versions of *inSTREAM*, for dates after 2037. Such future dates are sometimes used for synthesized data or hypothetical scenarios.)

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.

3.2.5 Fish ages and age classes

inSTREAM 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. Four age classes are used (although the number of classes can be changed via relatively simple modifications to the software; see the software guide):

- Age 0—fish that have not yet reached their first January 1.

- Age 1—fish that have survived one January 1.

- Age 2—fish that have survived the January 1 of two years.

- Age 3+—any fish that have survived the January 1 of more than two years.

3.2.6 Habitat dimensions and distances

X and Y dimensions. Version 6 of *inSTREAM* uses a general 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, but follow the conventions of the UTM system: coordinates are in meters, with X as the east-west dimension and X coordinates increasing from west to east, and Y increasing from south to north.

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.

3.2.7 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 *inSTREAM*, 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:

$$S = \frac{\exp(Z)}{1 + \exp(Z)}$$

where

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

$$LogistA = \frac{(LogistC - LogistD)}{(habVarAtS01 - habVarAtS09)}$$

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

$$LogistC = \ln\left(\frac{0.1}{0.9}\right)$$

$$LogistD = \ln\left(\frac{0.9}{0.1}\right).$$

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 5.4.)

4 Habitat Variables and Methods

Habitat is depicted in *inSTREAM* as a network of reaches, though often just one reach is used. Reaches are habitat objects that each represent a contiguous length or segment of river or stream. Cells are the smallest scale, objects that represent patches of relatively uniform habitat

within a reach. A model contains one or more reaches, and each reach is made up of many cells.

4.1 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.

4.1.1 Reach-scale variables

Habitat parameters: Habitat parameters are model equation coefficients that are constant over time and within a reach. These include the parameters used to calculate food production in each cell (Section 4.2.4). Two reach-level parameters affect fish spawning and feeding: the maximum flow at which trout will spawn (Section 5.1.1.5) and the fraction by which velocities are reduced for trout swimming in velocity shelters (Section 5.3.7). Two parameters relating flow to reach-scale bed shear stress are used in simulating redd mortality via scour and deposition (Section 6.1.2).

Time-series inputs: Reaches have four variables that are updated from input files: flow (m^3/s) and drift food concentration are updated each model step; temperature (˚C) and turbidity (NTU) are updated daily. Flow is used primarily to determine the depth and velocity in each of the reach's cells (Section 4.2.2). The wetted surface area of each reach is also updated each step from the flow; the reach area is simply the sum of the areas of all cells with depth greater than zero.

Day phase: This variable (which does not vary among reaches) represents whether the current simulation time is during day (reach variable dayPhase = DAY) or night (dayPhase = NIGHT). Updating of this variable is described below (Sect. 4.1.3)

Piscivorous fish density: The density of piscivorous trout in each reach, *piscivorousFishDensity* (number per cm^2), is used to model fish predation (Section 5.4.4). This variable is calculated as the number of piscivorous fish, divided by the reach's area. Reach area is evaluated each model step as the sum of the areas of all cells that have depth > 0 at the current daily flow. Whether a trout is piscivorous is determined by (1) whether it is feeding (hiding fish are assumed not piscivorous) and (2) a length threshold; the number of piscivorous fish varies over time as fish change activity and grow and die (Section 5.4.4). The value of *piscivorousFishDensity* for each reach is updated during the fish's activity and habitat selection action: after each trout executes this decision (in descending order of trout size), the model determines whether the trout is piscivorous and, if so, increases *piscivorousFishDensity* for the reach that the trout occupies.

Barriers: Model objects representing obstructions such as waterfalls or dams that prevent trout from moving upstream are not represented in version 6 of *inSTREAM*. (They were represented in some previous versions.)

4.1.2 Reach links

Users of *inSTREAM* 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 2).

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 2 illustrates ways that networks of reaches can be defined, and Table 1 describes how these networks are defined using junction numbers.
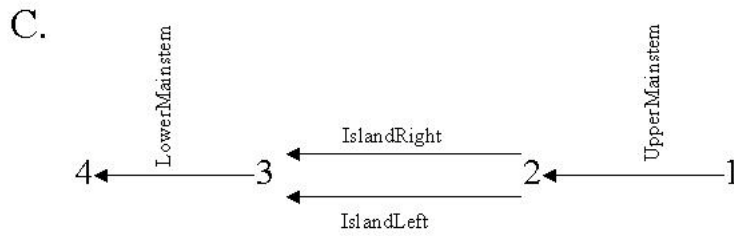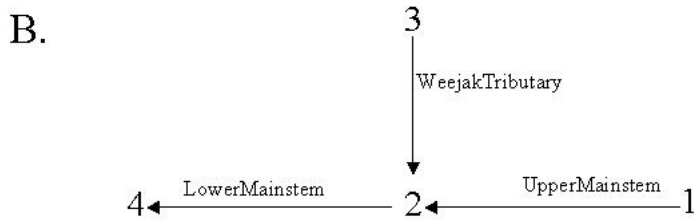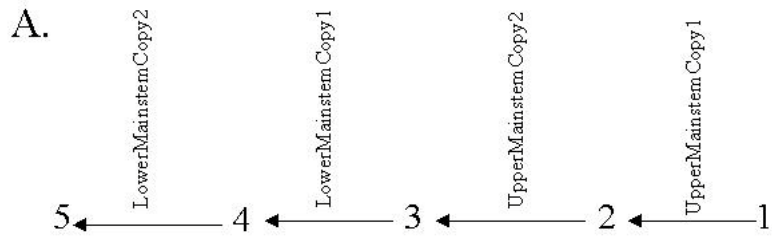
Figure 2. Example reach network configurations, showing junction numbers and reach names. Arrows represent reaches, pointing in the downstream direction. Network A has four sequential reaches generated by using two copies each of an upper and lower study site. Network B has two mainstem reaches and a tributary. Network C has reaches on either side of an island.

Table 1. 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

4.1.3 Sub-daily time steps

A key habitat-driven process in *inSTREAM-SD* is determining when each sub-daily time step starts. This process is executed by the model each hour; when the model determines that a new time step starts on the current hour, then "step" actions that end one time step and start another are executed. The key model variable *numHoursSinceLastStep* is updated with the number of hours since the previous step; this variable therefore is the length (h) of the time step that just ended.

Because *inSTREAM-SD* is designed to simulate how fish respond to within-day changes in flow and drift concentration, and to the difference between day and night, three events can trigger a step.

The first event is the switch between daytime and night. Daytime is assumed to start before sunrise and ends after sunset. The habitat parameter *habTwilightLength* is the number of hours that daytime is assumed to start before sunrise, and to extend after sunset. The variable *dayLength* is the number of hours between sunrise and sunset. A new variable *numberOfDaylightHours* is therefore equal to *dayLength* + (2 × *habTwilightLength*). A second new variable *numberOfNightHours* is equal to 24 minus *numberOfDaylightHours*.

Daytime therefore starts at a time (variable *daytimeStartTime*) equal to 12 (noon) minus (*numberOfDaylightHours*/2); and night starts at a time (variable *daytimeEndTime*) equal to 12

plus (*numberOfDaylightHours*/2). At each simulated hour, the model checks whether the start of day or start of night has occurred since the previous hour; if so, a new step is executed.

The day length (*dayLength*, number of hours of daylight, including twilight) is a calculated habitat variable. 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.

The second event that triggers a model step is a change in flow. If the flow in any reach has changed since the last time step by a specified amount, then a step is triggered. The change in flow that triggers movement is equal to the flow at the previous step (variable *flowAtLastMove*) times a model parameter *fracFlowChangeForMovement*. (The references to movement in these variable names are because simulated fish can only move at a model step.) If either of the following two conditions are met, then a step is triggered:

current flow > *flowAtLastMove* × (1 + *fracFlowChangeForMovement*)

or:

current flow < *flowAtLastMove* × (1 − *fracFlowChangeForMovement*).

The combination of flow- and daylight-triggered model steps means that there will be at least two time steps per day, and at sites with a simple one-peak hydropower generation cycle there will often be four time steps per day (unless the start or end of a generation flow peak coincides with the start or end of daytime).

The third event that can trigger a model step is a change in drift concentration. This potential trigger is included because rapid changes in flow can cause changes in drift concentration that do not parallel the flow changes (e.g., the observation of Miller and Judson 2014 that drift concentrations increased and then decreased during a several-hour period of increased but steady power-production flows), and we assume that trout can detect and respond to changes in drift concentration at time scales of one to several hours. The method for determining whether drift concentration triggers a step is identical to the method for flow, but a separate parameter is used for the fraction change in drift that triggers a step: the change in drift concentration that triggers a step is equal to the concentration at the previous step times a model parameter *fracDriftChangeForMovement*.

4.2 Cells

4.2.1 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. *inSTREAM* imports the corner coordinates of each cell. Any space not within a cell is treated as unavailable to the model fish.

Cells also have two variables for their distance to the upstream and downstream end of their reach. Evaluation and use of these variables is explained in Section 5.2.2.1.

4.2.2 Depth and velocity

The depth and velocity of each cell (and the number of cells that are submerged and therefore available to trout) vary with the reach's flow. A cell's water velocity is treated as a magnitude; the direction does not matter within *inSTREAM*.

To take advantage of existing stream hydraulic modeling software and avoid having to include hydraulic simulations, *inSTREAM* 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 (e.g., to aggregate hydraulic model results into larger cells), in GIS.

The input depth and velocity lookup tables should contain a wide range of flows. If *inSTREAM* 6 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 and possibly run-time errors that stop execution.

An example is depicted graphically in Figure 3. 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. This discontinuity in how velocity increases with flow is 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.)
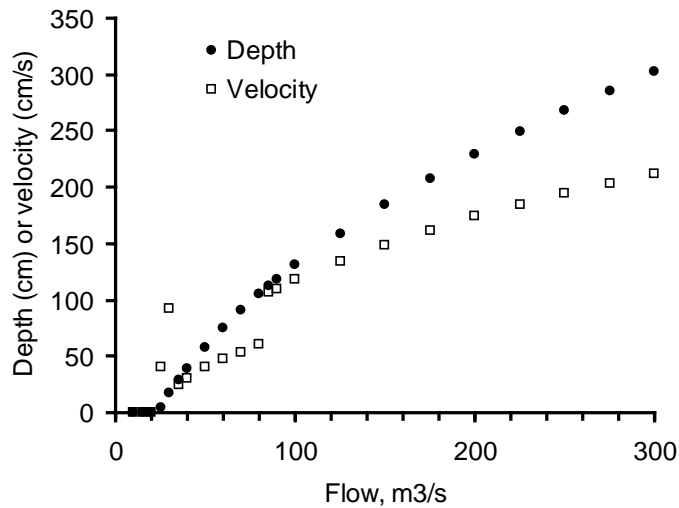
Figure 3. Example depth and velocity input for a cell. Each point represents an entry in the depth and velocity lookup table that is input for the cell.

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. 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; velocity, unlike depth, is assumed to approach zero as flow approaches zero. (Depth does not approach zero in pools.) Any channel margin cells that are submerged only at the highest flow in the lookup table can have unrealistically high projected velocities at flows above the highest lookup table flow. Cells submerged only at flows above the highest lookup table flows will always have zero depth and velocity (because all values in their lookup table are zero). The need to make these extrapolations can be avoided by making sure the lookup table includes flows both lower and higher than any occurring during a model run.

4.2.3 Velocity shelter availability

The availability of velocity shelters (which affect growth, Section 5.3.7; and high velocity mortality, Section 5.4.2) 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 trout 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; *inSTREAM* ignores this variability because of its complexity. Instead, *cellFracShelter* should represent drift feeding habitat for mid-sized to large trout.

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

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5.3.7). 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.)

4.2.1   Hiding cover availability

Because *inSTREAM-SD* (unlike other versions) represents hiding as a specific behavior that fish exhibit, it represents availability and competition for hiding space explicitly. Hiding cover availability is modeled just as velocity shelter is (Sect. 4.2.3). The fraction of cell area that provides hiding space is input (variable *cellFracHidingCover*). This input should reflect how much of each cell has hiding places such as aquatic vegetation and interstices among rocks. Like velocity shelter, the availability of hiding cover can vary with a fish's size, but this variability is ignored. Typically, *cellFracHidingCover* should represent hiding cover for mid-sized to large trout.

Cells keep track of their total hiding cover area (*cellFracHidingCover* × *cellArea*) and how much of that area is currently occupied by fish. Each fish using hiding cover occupies an area of shelter equal to the square of the fish's length. A fish has access to hiding cover if the unoccupied hiding cover area remaining in its cell is greater than zero. (If a cell contains some unoccupied hiding cover area but less than the square of the fish's length, the fish has access to cover in the cell, but zero remains available for subsequent fish.)

4.2.2 Spawning gravel availability

Spawning gravel availability is described as the fraction of cell area with gravel suitable for spawning, assumed to be constant over time. This area can include small pockets of gravel behind boulders as well as more classic spawning beds. This spawning gravel fraction (variable *cellFracSpawn*, a dimensionless fraction between zero and one) is provided as input for each cell.

4.2.3 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 5.4.5). The kind of habitat that trout can use for hiding varies with fish size. The terrestrial predation formulation is designed so that *cellDistToHide* should represent hiding for mid-sized to large trout.

4.2.4 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. *inSTREAM* 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 *inSTREAM* 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.

4.2.4.1 Production

In the absence of established models of trout food availability, *inSTREAM* uses models that are simple yet mechanistic and easily calibrated using observed trout 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 space.

In *inSTREAM-SD*, *habDriftConc* can vary over time and is read as input. Drift food concentration is an input so that *inSTREAM-SD* can evaluate assumptions about how sub-daily flow fluctuations affect the production and drift rates of food organisms. As in other versions, *habSearchProd* is assumed constant over time and treated as a habitat parameter.

[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 *inSTREAM* appears to generally capture the important dynamics of food competition.]

The trout feeding formulation uses hourly food production and consumption rates. 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:

$$driftHourlyCellTotal \ = \ 3600 \times cellArea \times cellDepth \times cellVelocity$$

$$\times \ habDriftConc \ / \ habDriftRegenDist.$$

This equation is modified from the one used by Railsback et al. (2009) for rectangular cells aligned with the current, by replacing numerator terms for cell width and length with the cell area. 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 length. Without this term, five cells 2 m^2 in area would have five times the food availability of one 10 m^2 cell. This term keeps the amount of food available from being an artifact of cell size.

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 5.3.3).

Estimation of values for these food parameters, including calibration, is discussed in Section 5.3.10.

4.2.4.2 Availability

The amount of food available to a particular trout affects the trout's habitat selection and growth methods (Section 5.2.1). 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 trout execute their habitat selection methods (Section 5.2), the rate of drift or search food consumed by any fish choosing to feed in 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 choosing to feed in 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.

5 Fish Variables and Methods

This section describes the methods used by the fish objects in *inSTREAM-SD*. Fish are one of the two trout life stages distinctly represented in the model; the other life stage—incubating eggs and alevins—are represented by redd objects (Section 6). Once fish have emerged from their redd, the methods and parameters they use do not vary with age.

Fish carry out four sets of actions: spawn, select a habitat cell and activity, 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 2.3.

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 or sites for which they were developed. Many parameter values, however, can be considered acceptable for stream trout 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.

5.1 Spawning

Spawning is included in *inSTREAM* because the model's objectives require simulation of the full life cycle and multiple trout generations, and of the effects of flow and temperature on reproduction. 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, *inSTREAM*'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, *inSTREAM*'s spawning methods simply force model trout to reproduce general spawning behaviors observed in real trout. Behaviors are included only if they appear important for simulating flow and temperature effects on reproduction or for representing the effects of spawning on the adult spawners.

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.

Spawning in Version 6 is more complex than in previous versions (including previous sub-daily versions). The additional complexity is to address the issue that trout spawning (especially, selecting a redd location and building the redd) is flow-dependent and can take longer than the one-hour minimum time step length. This version adds assumptions about how a female spawner considers flow variation over time in deciding whether and where to create a redd.

5.1.1 Decide whether to spawn

Once per day (at the first hour of daylight), each female trout determines whether it meets all of the fish- and habitat-based spawning criteria described below. These spawning criteria limit spawners to females of adequate size and physiological condition; and restrict spawning to physical conditions (dates, flows, temperatures) when spawning has been observed in real trout, 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 trout will spawn whether or not ideal gravel spawning habitat is present. This assumption is supported by observations reported by Magee et al. (1996).

On the days when all the spawning criteria are met for a female, then whether it actually spawns 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, which can be important to the population's reproductive success. Flow fluctuations during the spawning season can scour or dessicate redds of early spawners; if all spawning is early, then such events can eliminate the year's reproduction. The value of *fishSpawnProb* also gives the model user some control over what percent of spawning-sized fish actually spawn. If the inverse of *fishSpawnProb* is large compared to the number of days in the spawning period (e.g., 1/*fishSpawnProb* is greater than the number of potential spawning days), then it is likely that some potential spawners will not spawn.

A value of 0.04 appears generally reasonable for *fishSpawnProb*; it causes an average of 25 percent of ready fish to spawn in the first week of suitable conditions and 68 percent to spawn within 28 days of suitable conditions.

Once a female has decided to spawn, it starts a one-day process of selecting a cell for its redd. (This process is different from spawning cell selection in previous versions of inSTREAM.) Trout have a boolean variable *spawning* that is initialized to NO when they are created; this variable is set to YES when the trout decides to spawn. The spawner then identifies a list of cells that are suitable spawning habitat over the following day (including any flow changes), before choosing one and building its redd there (Sect. 5.1.2).

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The following subsections describe the spawning criteria. None of these criteria are well defined in the literature because trout spawning is difficult to observe. However, the criteria make ecological sense because they keep fish from spawning at times when their redds would be very vulnerable to mortality. The criteria are included in the model for the same reason: to represent the presumed ability of trout to avoid spawning under conditions that make successful incubation unlikely. The criteria include characteristics of both the fish and its habitat reach.

5.1.1.1 Minimum length, age, and condition

Because *inSTREAM* does not explicitly simulate the bioenergetics of reproduction, it uses fish length, age, and condition to predict energetic readiness to spawn. Minimum values of these characteristics are used to ensure that only fish with energy reserves comparable to those needed for gonad production can actually spawn. Length and condition are the primary indicators of spawning readiness as they are related to energy reserves, but the age minimum is useful in model runs where fish growth and condition are not well calibrated. Fish cannot spawn unless their age is at least equal to the value of the parameter *fishSpawnMinAge*, an integer age in years.

The model's fish cannot spawn until they attain a length equal to the parameter *fishSpawnMinLength*. (This parameter is also a key variable in the "Expected Reproductive Maturity" fitness measure used as a basis of habitat and activity selection decisions; Section 5.2.3.)

Finally, for a fish to spawn its condition factor (Section 5.3.1) must exceed the minimum condition factor parameter *fishSpawnMinCond* (unitless). Keeping in mind (a) the non-standard definition of condition factor (Section 5.3.1), (b) that the growth formulation makes condition less than 1.0 on any days when fish did not obtain at least as much energy as expended for respiration, and (c) that the bioenergetics of reproduction are not explicitly represented and fish have no incentive to put on weight in anticipation of spawning, the value of *fishSpawnMinCond* is recommended to be slightly less than 1.0; a value of 0.98 is typically used.

Values for *fishSpawnMinAge* and *fishSpawnMinLength* can vary considerably among sites and can often be estimated from site-specific census data. For cutthroat trout in the relatively small, infertile Little Jones Creek, Railsback and Harvey (2001) used 1 y for *fishSpawnMinAge*: field observations indicated that spawning in age 1 trout occurs, if rarely. Railsback and Harvey (2001) used a value of 12 cm for *fishSpawnMinLength*, on the basis of field observations and literature from similar sites. Meyer et al. (2003) provides data on how these spawning age and size parameters can vary with habitat conditions, in cutthroat trout. This variation can be large; for example Meyer et al. (2003) found that trout in the large South Fork Snake River did not mature until they were 30 cm long and five years old.

5.1.1.2 Not spawned this season

Trout are assumed not to spawn more than once per annual spawning season. The fish (both males and females) in *inSTREAM* have a boolean (yes-no) variable *spawnedThisSeason*. At the start of the first day of the spawning season, *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.)

5.1.1.3 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. Therefore, in *inSTREAM* 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.) Examples values are in Table 2.

Table 2. Example parameter values for spawning date window.

Species and site	*fishSpawnStartDate*	*fishSpawnEndDate*
Cutthroat trout, Little Jones Creek, coastal California (Railsback and Harvey 2001)	4/1	5/31
Rainbow trout, Tule River, Sierra Nevada California (Van Winkle et al. 1996)	4/1	6/30
Brown trout, Tule River, Sierra Nevada California (Van Winkle et al. 1996)	10/1	12/31

5.1.1.4 Temperature range

Temperature is widely accepted as a factor controlling the timing of 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 *inSTREAM* can only occur within a range defined by parameters for maximum and minimum spawning temperatures for spawning. Parameter values developed by Van Winkle et al. (1996) are in Table 3. For cutthroat trout at the Little Jones Creek study site, a value of 7° is used for *fishSpawnMinTemp* because spawning has been observed at approximately this temperature.

Table 3. Parameters and example values for spawning temperature range. Source: Van Winkle et al. (1996).

Parameter	Definition	Rainbow trout value	Brown trout value
fishSpawnMinTemp	Minimum temperature at which spawning occurs (°C)	8	4
fishSpawnMaxTemp	Maximum temperature at which spawning occurs (°C)	13	10

5.1.1.5 Flow limit

The maximum flow limit implements the assumption that fish will not spawn during high flow events. During unusually high flow, cells with depths and velocities suitable for redds (Section 5.1.2) 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.

5.1.1.6 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:

$$fracFlowChange = abs(reachFlow - yesterdaysFlow)/todaysFlow$$

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*.

These flow variables are daily mean flows, even in *inSTREAM-SD* which uses hourly flow input.

5.1.2 Select spawning cell and move there

Female spawners select the cell in which they then build a redd. This process is modified from previous versions of inSTREAM to consider within-day flow fluctuations: we assume that spawners will create redds only in cells that remain suitable for spawning continuously through all flows occurring over one day, from the model step at which the trout decides to spawn until the first daytime step of the following day.

While selection of habitat for foraging is modeled very mechanistically (Section 5.2), 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 trout. This design was chosen 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 *inSTREAM*'s objectives (Section 5.1). We do, however, need a simple representation of how flow affects where redds are placed because a redd's location affects its survival of dewatering (Section 6.1.1) and the habitat conditions that its newly emerged juveniles are exposed to.

On the model step at which a female decides to spawn, it identifies all cells that are currently suitable spawning sites. First, the model trout identifies a list of potential spawning cells using the same method used for destination cells during habitat selection (Section 5.2.2). However, for spawning in inSTREAM Version 6 we include all cells within two times the habitat selection radius; this larger radius is used because we assume spawners should be willing to expend considerable effort on this crucial behavior and because flow fluctuations are likely to reduce the availability of cells suitable for spawning.

For simulations with multiple habitat reaches, the potential spawning sites could include cells in a different reach from the spawner's current cell. Cells in another reach could be chosen for a redd even if the habitat criteria for spawning (Section 5.1.1) are not all met in that other reach. For example, a female can decide to spawn only when habitat criteria such as temperature (Section 5.1.1.4) are met in its current reach, but the female could then spawn in a reach where the temperature criterion is not met. This possibility remains in *inSTREAM* only because it was judged not important enough to justify the additional logic and computation to prevent it.

This formulation does not cause, or allow, long spawning migrations. Typical applications of *inSTREAM* are expected to have too few and small reaches to represent long-distance migrations anyway.

After creating a list of cells within two times the habitat selection radius, the spawner removes from this potential spawning cell list all cells with either (a) a value of zero for cell variable *cellFracSpawn*; (b) velocity suitability (described below) less than 0.1; or (c) depth suitability less than 0.1. The list therefore becomes a list of cells with at least marginal suitability for spawning.

On each model step, any female trout with a value of YES for *spawning* (except those that set *spawning* to YES on the current step) examines its list of potential spawning cells and removes those with depth or velocity suitability values of less than 0.1 at the current flow. This process causes spawners to eliminate cells that are not suitable at all flows over the full day after they decide to spawn.

Female trout with *spawning* set to YES at the start of the first daytime model step (those that decided to spawn one day earlier) then rate the cells on their list of potential spawning cells to identify the cell where the redd will be created. If this list is empty (no potential cell has been suitable over all of the previous day), then the trout does not spawn: its value of *spawning* is set back to NO and, starting on the current step, it repeats the entire spawning decision process.

If the list of potential spawning cells is not empty, the spawning cell is chosen as the one with the highest value of variable *spawnQuality* where:

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

The variables *spawnDepthSuit* and *spawnVelocitySuit* are unitless habitat suitability factors determined using methods described below. The value of *spawnGravelArea* is the cell area times its fraction with spawning gravel (*cellArea* × *cellFracSpawn*). (The units of *spawnQuality* are therefore cm^2, but they are unimportant.) The variable *spawnGravelArea* 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 6.1.5) 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.

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 trout 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

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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 *inSTREAM* 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 4), which are example values for relatively small stream trout. These parameter values were estimated from a collection of rainbow and brown trout spawning criteria (PG&E 1994). The number of points in this suitability relationship is fixed at five.

Table 4. Example parameter values for spawning depth suitability. 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	5	*fishSpawnDSuitS2*	0.0
fishSpawnDSuitD3	50	*fishSpawnDSuitS3*	1.0
fishSpawnDSuitD4	100	*fishSpawnDSuitS4*	1.0
fishSpawnDSuitD5	1000	*fishSpawnDSuitS5*	0.0
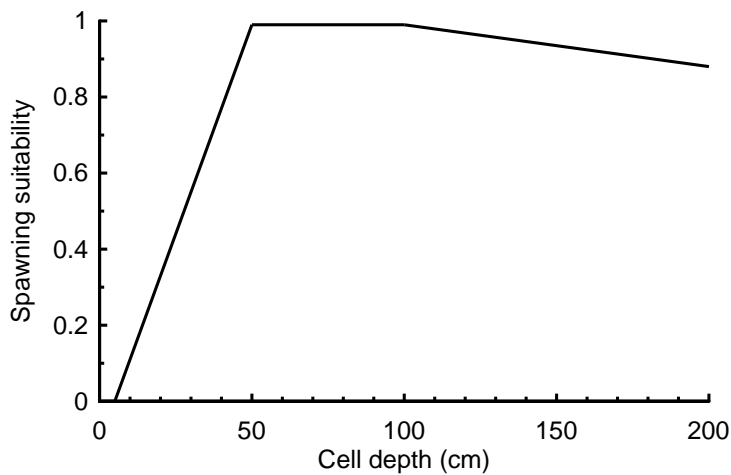
Figure 4. Spawning suitability function for depth.

A value of *spawnVelocitySuit* for a cell is interpolated from the five pairs of parameters in Table 5, which includes example parameter values for small trout. The parameter values in Table 5 (plotted in Figure 5) were estimated from several brown trout spawning criteria (PG&E 1994). The number of points in this relationship is fixed at six.

Table 5. Example parameter values for spawning velocity suitability. 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	10	*fishSpawnVSuitS2*	0.0
fishSpawnVSuitV3	20	*fishSpawnVSuitS3*	1.0
fishSpawnVSuitV4	75	*fishSpawnVSuitS4*	1.0
fishSpawnVSuitV5	100	*fishSpawnVSuitS5*	0.0
fishSpawnVSuitV6	1000	*fishSpawnVSuitS6*	0.0
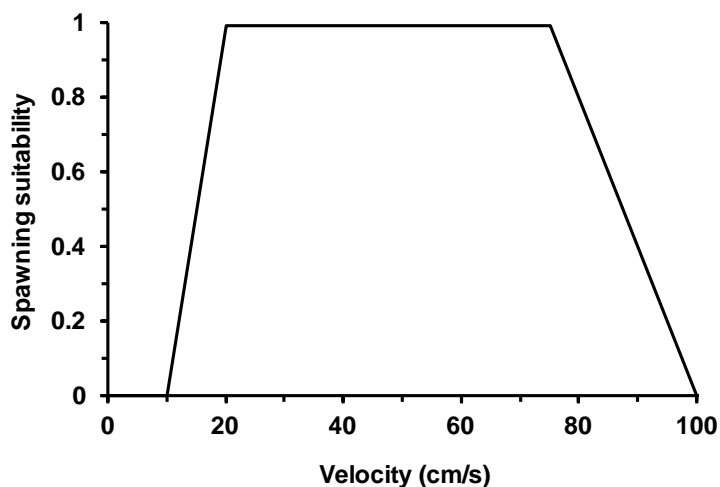
Figure 5. Spawning suitability function for velocity.

These example parameter values should be reconsidered for each site that *inSTREAM* 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. To keep spawners from selecting cells with large areas of marginal

spawning suitability instead of small cells of high suitability, it is desirable for the suitability relations to be steep-sided instead of having wide ranges of intermediate suitability.

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.)

When the female spawner has selected its spawning cell, the spawner moves to that cell. (The only effect this has on the spawner is that when it executes its habitat selection action later the same day, it will start from the cell it spawned in.) Male spawners are not assumed to move to the spawning cell.

5.1.3 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. Van Winkle et al. (1996) developed values of *fishFecundParamA* and *fishFecundParamB* for brown trout from Avery (1985), which appear generally useful for relatively small stream-resident trout. These values (Table 6, brown trout values) result in fecundities of 60 eggs for a small spawner of 12 cm and 220 eggs for a spawner of 20 cm, corresponding well with citations provided by Carlander (1969). Meyer et al. (2003) developed parameters for fecundity from 26 observations of resident cutthroat trout, with lengths between 10 and 30 cm. The total lengths reported by Meyer et al. were converted to fork length by applying a ratio of 0.97 (Carlander 1969). The resulting parameter values (Table 6, cutthroat trout values) produce fecundities approximately 50 percent higher than those of Van Winkle et al. (1996). The differences between the two parameter sets reported in Table 6 may be more a result of random variation or differences among sites than real differences among trout species.

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 6.1). 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, and concluded 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.

Table 6. Parameter values for fecundity.

Parameter	Definition	Species	Value
fishFecundParamA	Fecundity (eggs per redd) multiplier	Brown *	0.11
		Cutthroat**	0.18
fishFecundParamB	Fecundity exponent	Brown *	2.54
		Cutthroat**	2.51
fishSpawnEgg Viability	Fraction of female's eggs that become viable eggs in the redd.	(unlikely to vary with species)	0.8

* Source: Van Winkle et al. (1996)

**Source: Meyer et al. (2003)

5.1.4 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 trout that:

- Is male;

- Is of the same species as the female;

- Occupies the same reach as the female's new redd;

- Has length greater than the parameter *fishSpawnMinLength*;

- Has age equal to or greater than the parameter *fishSpawnMinAge*;

- Has condition greater than the parameter *fishSpawnMinCond*; and

- Has not previously spawned during the current spawning season.

5.1.5 Incur weight loss

Spawning involves a significant penalty in body mass and energy. Hayes et al. (2000) cites literature indicating a typical loss of 18% of mass and 45% of energy content upon spawning in trout, for both males and females (e.g., Lien 1978). This energy loss can significantly affect the habitat selection and survival (especially of starvation) of spawners, so it is included in *inSTREAM*. When any trout—male or female—spawns, their weight is reduced according to the parameter *fishSpawnWtLossFraction*. Fish weight is multiplied by 1- *fishSpawnWtLossFraction*. A value of 0.2 for *fishSpawnWtLossFraction* is supported by Hayes et al. (2000). The spawner's condition factor is then updated with the new weight, so it affects habitat selection in the current time step.

Figure 6 represents how the probability of surviving starvation and disease (Section 5.4.6) for 90 days varies with the value of *fishSpawnWtLossFraction*, using the feeding, growth, and survival parameters described in this report for cutthroat trout. The figure indicates that a 20% loss of body weight during spawning reduces the probability of surviving starvation and disease for 90 days by about 10-15%.
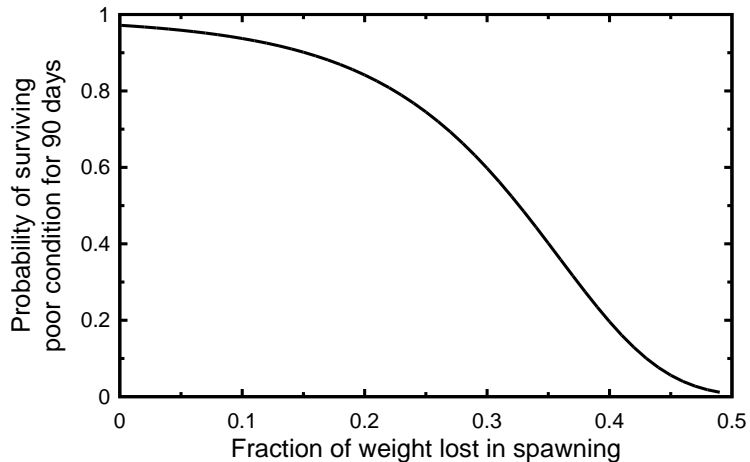
Figure 6. Probability of surviving starvation for 90 d, as a function of spawning weight loss. A 15-cm trout feeding in velocity of 40 cm/s with velocity shelter is represented.

5.2 Habitat and Activity Selection

One of the fundamental differences between *inSTREAM-SD* and other versions of *inSTREAM* is including activity selection with habitat selection as the key adaptive trait of trout. Railsback et al. (1999) discussed the importance of habitat selection (also referred to, imprecisely, as "movement"), reviewed methods used in previous models, and developed the approach used in *inSTREAM*. Railsback et al. (2006; section A.2.1.4) developed and discussed several approaches for including activity selection with habitat selection in a combined adaptive trait, and explain why the approach used in *inSTREAM-SD* was chosen. The ability of this approach to reproduce diverse patterns of response to environmental and competitive conditions observed in real trout was demonstrated by Railsback et al. (2005).

The habitat and activity selection trait is conceptually simple: every model step, each trout selects the habitat cell and activity that (1) is close enough that the fish can be assumed to be aware of conditions in it, and (2) offers the highest "Expected Reproductive Maturity" (ERM; expected probability of surviving over a time horizon × expected fraction of reproductive size at

the end of the time horizon). Other versions of *inSTREAM* assume that fish are active only in the day, so the trout select habitat to maximize ERM during daytime conditions. For *inSTREAM-SD*, we assume fish can be active day or night, and select their daytime and night habitat separately to maximize overall ERM.

Fish are assumed to maximize the ERM resulting from both daytime and night conditions, while choosing (1) which habitat cell to use during each of the two phases, and (2) whether to actively feed or hide during each phase. Fish choose among four options.

- Feeding in the best cell during the daytime and hiding in the safest cell at night,
- Feeding in the best cell during daytime and feeding in the best cell at night (these cells could be different),
- Hiding in the safest available cell during the daytime and feeding in the best cell at night, or
- Hiding during both daytime and night.

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

5.2.1 Competition for resources via dominance hierarchy

The trait assumes a size-based dominance hierarchy: fish can only use resources (food, velocity shelters, hiding cover) 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 *inSTREAM* by executing the habitat selection method in order of descending fish length. The longest individual selects its cell and activity first, and the food and velocity shelter, or hiding cover, it uses are subtracted from what remains available in the cell for additional trout. Subsequent trout therefore base their decisions not on the total resources in each cell but on the resources remaining unconsumed by larger fish.

Two elements of competition for food or space are not included in *inSTREAM*. Some literature indicates that there may be inherent differences among species in dominance: individuals of one species may outcompete larger individuals of another species (e.g., Volpe et al. 2000, Magoulick and Wilzbach 1999). In some earlier trout IBMs (Van Winkle et al. 1996; earlier versions of *inSTREAM*) the relative dominance of an individual could be a function of its species as well as its length. Similarly, some literature indicates that individuals have an inherent tendency to stay in one location ("site fidelity") and that prior residence of a site increases the ability of a trout to defend the site from larger competitors (Cutts et al. 1999, Johnsson et al. 1999, Volpe et al. 2000). However, neither species nor prior residence effects on dominance are clearly universal; and it is possible for them to be reproduced in an IBM without being hardwired in. For example, one species may appear to out-compete another simply because it spawns earlier in the year and so has a size advantage. Young (2003), for example, found size to be the dominant factor determining dominance among a mix of coho salmon and steelhead individuals. Large trout may appear to exhibit site fidelity simply because their habitat offers very high fitness under a wide range of flows and temperatures, so they rarely have incentive to move. These two elements of competition are not explicitly included in *inSTREAM* because they are not clearly important and because doing so would require assumptions and parameters for which there is little basis.

5.2.2 Identification of potential destination cells

When each individual trout 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.

5.2.2.1 Distance limitation

Only habitat cells within a certain distance (as defined in Section 3.2.6) 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 time step of several hours. 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 *inSTREAM*, 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 (Bowen 1996, 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 (m/d) 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 adult trout commonly move distances up to 300 m. 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. Diana et al. (2004) observed large brown trout that routinely moved between stream locations more than 500 m apart.

Parameter values for a mid-sized, moderate-gradient stream (Table 7) estimate *maxMoveDistance* as less than 2 m for newly emerged trout with length of 3 cm, as 5 m for juveniles 5 cm long, as 30 m for trout 10 cm long, and 80 m for trout 20 cm long. (These parameters can strongly affect execution speed, because the number of cells each trout

evaluates in habitat and activity selection—the most computationally intense process in the model—increases more than linearly with *maxMoveDistance.*)

Table 7. Example parameter values for fish movement distance.

Parameter	Definition	Value
fishMoveDistParamA	Multiplier for maximum movement distance (unitless)	20
fishMoveDistParamB	Exponent for maximum movement distance (unitless)	2
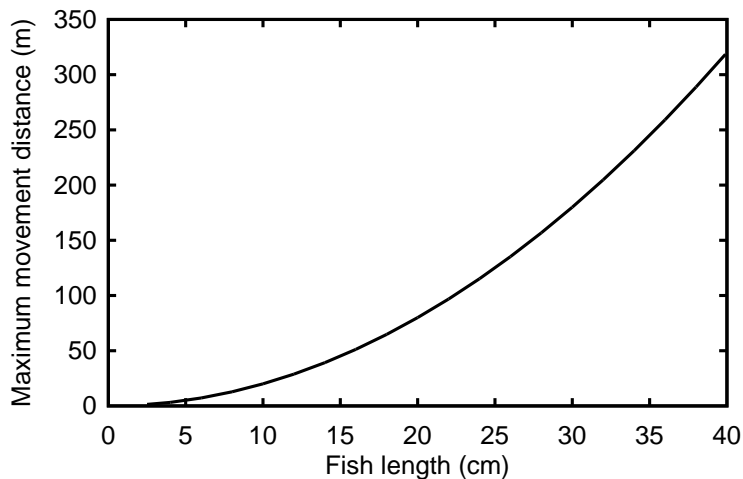
Figure 7. The maximum distance fish can move, as a function of their length, for *fishMoveDistParamA* = 20, *fishMoveDistParamB* = 2. Note that the Y axis is in meters.

If a simulation includes more than one habitat reach, then cells in adjacent reaches may also be potential movement destinations for a trout. 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 *inSTREAM* 6 is very simple: manually identifying the cells at the upstream and downstream ends of each reach during input preparation, and using straight-line distances from cells to the nearest such end cell. Specifically:

1. 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 as part of preparing the cell input, and input via the cell data file (see the software guide). 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.

2. 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.

3. 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 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.

5.2.2.2 Barriers
Barriers to upstream or downstream movement are not implemented in *inSTREAM* 6.

5.2.2.3 Minimum depth
Cells are excluded as destinations if they have depth ≤ 0, with the exception that the fish's current cell is included if there are no non-dry cells within the maximum movement distance. This criterion is imposed to reduce computer execution: the fitness measure that fish used to evaluate potential destinations (Section 5.2.3) provides a very strong incentive to avoid moving to dry cells, where survival probabilities are extremely low and food intake zero. However, specifically excluding movement to dry cells significantly reduces the computations needed to select a destination cell.

Fish are not required to move out of their current cell if its depth drops to zero, but again they will have a strong incentive to move. 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 5.4.3 concerning stranding mortality.)

5.2.3 Evaluation of potential destination cells

A fish evaluates each potential destination cell to determine the ERM (fitness) it would provide, for each of the four combinations of day and night activity.

5.2.3.1 Memory variables

The fish have four memory variables that are used in movement decisions. Net energy intake (which is proportional to growth rate) is used instead of growth because the trout model software uses net energy in the habitat and activity selection decision trait; there is no need in these methods to convert net energy to growth. (The exact meaning of these memory variables is determined by the methods for giving them values, discussed below.)

- *netEnergyForFeedingLastPhase* is the hourly net energy intake rate (j/h) that the fish experienced while feeding during the previous phase, *or* the net energy intake the fish would have experienced had it chosen to feed in the best cell for feeding;
- *survivalForFeedingLastPhase* is the daily survival probability that the fish experienced while feeding during the previous phase, *or* the survival rate the fish would have experienced had it chosen to feed in the best cell for feeding;
- *netEnergyForHidingLastPhase* is the hourly net energy intake rate (j/h) that the fish experienced while hiding during the previous phase, *or* the net energy intake the fish would have experienced had it chosen to hide in the best cell for hiding; and
- *survivalForHidingLastPhase* is the daily survival probability that the fish experienced while hiding during the previous phase, *or* the survival rate the fish would have experienced had it chosen to hide in the best cell for hiding.

When fish are initialized at the start of a simulation, these memory variables are set to neutral values: *netEnergyForFeedingLastPhase* and *netEnergyForHidingLastPhase* are initialized to zero, and *survivalForFeedingLastPhase* and *survivalForHidingLastPhase* are initialized to 1.0. This initialization method starts the model with no inherent bias towards feeding or hiding during the first phase simulated, but also means that the model may need to run for several days before diel movements are realistic. Updating these memory variables during a simulation is discussed below.

5.2.3.2 Habitat and activity decision

The habitat and activity selection trait uses the following steps to evaluate each potential destination cell.

- The fish determines whether it would have access to hiding cover if it chose to hide in the cell, using the approach described in Section 4.2.1. The variable *isHideCoverAvailable* is set to YES or NO accordingly.
- The fish calculates the hourly net energy intake rate it would obtain if it fed in the cell (*hourlyNetEnergyIfFeed*, j/h). This rate is calculated using the feeding and bioenergetics methods, which includes determining whether the fish uses the search or drift feeding strategies (Section 5.3), considering the effect of night on food intake rates.
- The fish calculates the net energy intake rate it would obtain if it hid in the cell (*hourlyNetEnergyIfHide*, j/h). This rate, which will always be negative, is also calculated using the feeding and bioenergetics models with the following assumptions. Food intake is zero. The feeding strategy is set to "HIDE" (there are two fish variables, *cellFeedingStrategy* and *fishFeedingStrategy*, which can be set to 0 or 1 for DRIFT and SEARCH, or -1 for HIDE). The respiration costs are calculated assuming a swim speed of zero (Section 5.3.7).

- The fish calculates the daily non-starvation survival probability it would experience if it fed in the cell (*dailySurvivalIfFeed*, unitless). This probability depends on whether it is day vs. night, and assumes the fish is feeding, not hiding in cover (Section 5.2.5.1).
- The fish calculates the daily non-starvation survival probability for hiding in the cell (*dailySurvivalIfHide*, unitless). This probability is calculated the same way as *dailySurvivalIfFeed*, except that some survival probabilities depend on the value of *isHideCoverAvailable*– if the fish has hiding cover available, then survival is increased (Section 5.4).
- The fish calculates its ERM in the cell for the four possible combinations of feeding and hiding. These calculations use one set of equations (defined in Sect. 5.2.5) and inputs to the equations that vary for the four combinations (and whether the current phase is day or night). The inputs for each combination are defined in Table 8. Note that these calculations are based on the expected <u>daily</u> growth and survival, and do not depend on how many hours are actually in the model time step being simulated. They make use of day length variables defined in Section 4.1.3. The total daily net energy intake (*dailyNetEnergy*, j/d) is equal to:

$$(netEnergyDay \times numberOfDaylightHours) + (netEnergyNight \times numberOfNightHours).$$

The total daily non-starvation survival probability (*dailyNonStarveSurvival*, unitless) is calculated as an average over the day (which is mathematically equivalent to converting survival to hourly mortality and summing mortality over day and night periods). The value of *dailyNonStarveSurvival* is:

$$\left[(survivalDay \times numberOfDaylightHours) + (survivalNight \times numberOfNightHours)\right]/24 \, .$$

The value of ERM for each combination of feeding and hiding is calculated as described in Sect. 5.2.5. The probability of surviving non-starvation risks over the time horizon is equal to *dailyNonStarveSurvival* raised to the time horizon power. The value of *dailyNetEnergy* is used to calculate the probability of surviving starvation over the time horizon and the fraction of reproductive length the fish will be at the end of the horizon.

If the best ERM for the cell (the best of the four combinations of feeding and hiding) is better than the best ERM for previously evaluated cells, then the cell becomes the new candidate destination cell.

After evaluating all potential destination cells in this manner, the fish moves to the one offering highest ERM. It also assumes the strategy (drift or search feeding, or hiding) that provided the highest ERM. Its use of velocity shelter or hiding cover area is deducted from that available in the destination cell.

Table 8. Inputs for ERM calculations.

Current Phase	Daytime Activity	Night Activity	netEnergyDay	netEnergyNight	survivalDay	survivalNight
Day	FEED	HIDE	*hourlyNetEnergyIfFeed*	*netEnergyForHidingLastPhase*	*dailySurvivalIfFeed*	*survivalForHidingLastPhase*
	FEED	FEED	*hourlyNetEnergyIfFeed*	*netEnergyForFeedingLastPhase*	*dailySurvivalIfFeed*	*survivalForFeedingLastPhase*
	HIDE	HIDE	*hourlyNetEnergyIfHide*	*netEnergyForHidingLastPhase*	*dailySurvivalIfHide*	*survivalForHidingLastPhase*
	HIDE	FEED	*hourlyNetEnergyIfHide*	*netEnergyForFeedingLastPhase*	*dailySurvivalIfHide*	*survivalForFeedingLastPhase*
Night	FEED	HIDE	*netEnergyForFeedingLastPhase*	*hourlyNetEnergyIfHide*	*survivalForFeedingLastPhase*	*dailySurvivalIfHide*
	FEED	FEED	*netEnergyForFeedingLastPhase*	*hourlyNetEnergyIfFeed*	*survivalForFeedingLastPhase*	*dailySurvivalIfFeed*
	HIDE	HIDE	*netEnergyForHidingLastPhase*	*hourlyNetEnergyIfHide*	*survivalForHidingLastPhase*	*dailySurvivalIfHide*
	HIDE	FEED	*netEnergyForHidingLastPhase*	*hourlyNetEnergyIfFeed*	*survivalForHideingLastPhase*	*dailySurvivalIfFeed*

5.2.3.3 Memory Variables Update

During evaluation of each potential destination cell, the memory variables are also updated. How the memory variables are updated is very important to the habitat and activity selection trait.

The memory variables are intended to represent, at any time, the conditions the fish experienced at the end of the previous phase. Because flow changes can trigger movement within a phase, a fish does not know at the time it moves whether or not the current model step is the last one within the current phase. Therefore, memory variables cannot be updated until the start of a new phase, at which time the fish knows that the immediately preceding conditions were from the end of the previous phase. For example, if fish move at mid-day as the result of a flow change, then they base their decisions on memory variables that were *not* updated at the previous step (which was also in daytime); instead, they need to use memory variables updated at the end of the preceding night. The following approach accommodates this need by using temporary memory variables that only replace the real memory variables when movement is conducted at the start of a new phase. The temporary memory variables are *tempNetEnergyIfFeed*, *tempNetEnergyIfHide*, *tempSurvivalIfFeed*, and *tempSurvivalIfHide*, corresponding to the four memory variables used in the above movement method.

The following methods are used in updating the memory variables as the fish evaluates each cell as a destination.

- At the start of habitat selection, the fish determines whether it is the start of a new daytime/night phase. If the model step was triggered by a new phase, then the four memory variables are replaced by the values of the corresponding temporary memory variables. If the step is due to a flow change, then the memory variables are unchanged.

- The four temporary memory variables, plus two other temporary variables (*tempBestERMForFeed* and *tempBestERMForHide*) are initialized to a large negative number before a fish starts evaluating potential destinations.

- If the current phase is daytime, the ERM for the daytime-feed, night-hide activity combination for each cell is compared to the value of *tempBestERMForFeed*. If the cell's ERM for this activity combination is greater than *tempBestERMForFeed*, then the value of *hourlyNetEnergyIfFeed* for the cell replaces *tempNetEnergyIfFeed*, the value of *dailySurvivalIfFeed* for the cell replaces the current value of *tempSurvivalIfFeed*, and *tempBestERMForFeed* is replaced by the cell's ERM for this activity combination.

- If the current phase is daytime, the ERM for the daytime-feed, night-feed activity combination is compared to the value of *tempBestERMForFeed*. If the cell's ERM for this activity combination is greater than *tempBestERMForFeed*, then the value of *hourlyNetEnergyIfFeed* for the cell replaces *tempNetEnergyIfFeed*, the value of *dailySurvivalIfFeed* for the cell replaces the current value of *tempSurvivalIfFeed*, and *tempBestERMForFeed* is replaced by the cell's ERM for this activity combination.

- If the current phase is daytime, the ERM for the daytime-hide, night-feed activity combination is compared to the value of *tempBestERMForHide*. If the cell's ERM for this activity combination is greater than *tempBestERMForHide*, then the value of *hourlyNetEnergyIfHide* for the cell replaces *tempNetEnergyIfHide*, the value of *dailySurvivalIfHide* for the cell replaces the current value of *tempSurvivalIfHide*, and *tempBestERMForHide* is replaced by the cell's ERM for this activity combination.

- If the current phase is daytime, the ERM for the daytime-hide, night-hide activity combination is compared to the value of *tempBestERMForHide*. If the cell's ERM for this activity combination is greater than *tempBestERMForHide*, then the value of *hourlyNetEnergyIfHide* for the cell replaces *tempNetEnergyIfHide*, the value of *dailySurvivalIfHide* for the cell replaces the current value of *tempSurvivalIfHide*, and *tempBestERMForHide* is replaced by the cell's ERM for this activity combination.

- If the current phase is night, the ERM for the daytime-feed, night-hide activity combination is compared to the value of *tempBestERMForHide*. If the cell's ERM for this activity combination is greater than *tempBestERMForHide*, then the value of *hourlyNetEnergyIfHide* for the cell replaces *tempNetEnergyIfHide*, the value of *dailySurvivalIfHide* for the cell replaces the current value of *tempSurvivalIfHide*, and *tempBestERMForHide* is replaced by the cell's ERM for this activity combination.

- If the current phase is night, the ERM for the daytime-feed, night-feed activity combination is compared to the value of *tempBestERMForFeed*. If the cell's ERM for this activity combination is greater than *tempBestERMForFeed*, then the value of *hourlyNetEnergyIfFeed* for the cell replaces *tempNetEnergyIfFeed*, the value of *dailySurvivalIfFeed* for the cell replaces the current value of *tempSurvivalIfFeed*, and *tempBestERMForFeed* is replaced by the cell's ERM for this activity combination.

- If the current phase is night, the ERM for the daytime-hide, night-feed activity combination is compared to the value of *tempBestERMForFeed*. If the cell's ERM for this activity combination is greater than *tempBestERMForFeed*, then the value of *hourlyNetEnergyIfFeed* for the cell replaces *tempNetEnergyIfFeed*, the value of *dailySurvivalIfFeed* for the cell replaces the current value of *tempSurvivalIfFeed*, and *tempBestERMForFeed* is replaced by the cell's ERM for this activity combination.

- If the current phase is night, the ERM for the daytime-hide, night-hide activity combination is compared to the value of *tempBestERMForHide*. If the cell's ERM for this activity combination is greater than *tempBestERMForHide*, then the value of *hourlyNetEnergyIfHide* for the cell replaces *tempNetEnergyIfHide*, the value of *dailySurvivalIfHide* for the cell replaces the current value of *tempSurvivalIfHide*, and *tempBestERMForHide* is replaced by the cell's ERM for this activity combination.

5.2.4 Selection of best cell and activity

The fish identifies the combination of cell and activity that has the highest value of the expected maturity fitness measure, and then moves there and executes the activity. When a fish moves into a cell, the resources it uses are subtracted from those available for subsequent fish (sections 4.2.3; 4.2.4). These resources may include one of the two kinds of food, velocity shelter, or hiding cover. 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.

5.2.5 Calculation of Expected Reproductive Maturity in *inSTREAM* 6

Individual fish select the cell and activity providing the highest value of ERM, represented in the model by the variable *expectedMaturity* where:

$$expectedMaturity = nonstarvSurvival \times starvSurvival \times lengthFunc$$

All versions of *inSTREAM* use a form of *expectedMaturity* but the exact formulation differs among versions. The following subsections describe the components of *expectedMaturity* in *inSTREAM* 6.

5.2.5.1 Survival of mortality other than starvation

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:

$$nonstarvSurvival = dailyNonStarveSurvival^{fishFitnessHorizon}$$

The formulation of *nonstarvSurvival* implicitly assumes that trout consider all mortality sources in their habitat selection decision. However, *inSTREAM-SD* includes one exception: angler harvest is included as a mortality source, but fish are assumed not to be aware of this risk and not to consider it in selecting habitat and activity. This means that the trout 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 in *inSTREAM*, except for angler harvest.

5.2.5.1 Survival of starvation

In the equation for *expectedMaturity*, the value of *starvSurvival* is the probability of surviving the risk of poor condition (closely related to starvation; Section 5.4.6) 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 *expectedMaturity* using the simple prediction that the current day's growth rate would persist over the time horizon.

- Calculate daily growth (g/d) from *dailyNetEnergy* (j/d) by dividing *dailyNetEnergy* by the fish parameter *fishEnergyDensity* (j/g).

- Project the fish's weight, length, and condition factor *fishCondition* (Section 5.3.1) 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 5.3.1.

- 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 5.4.6):

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

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 3.2.7) 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.

5.2.5.2 Effect of length on expected fitness

The final term in the equation for *expectedMaturity* is *lengthFunc*, which represents the effect of a fish's length on its fitness over the time horizon. Other versions of *inSTREAM* represent this effect using a term *fracMature*, which represents how close to the size of sexual maturity a fish would be at the end of the fitness time horizon. While that approach produces realistic behavior and growth in versions using a one-day time step, it does not when we assume fish also choose whether to feed or hide each day and night: fish would choose to feed only enough to avoid starvation and hide the rest of the time, producing no growth. In reality, trout in many rivers grow to sizes far greater than the minimum to reproduce.

Instead, *inSTREAM-SD* represents the effects of length on fitness as a function reflecting how fitness potential varies with the fish's expected length at the end of the time horizon. This length function models how expected fitness increases with the length the fish expects to attain by the end of the time horizon, a function of its growth rate.

The length function is justified by both empirical and theoretical considerations. First, some kind of function encouraging fish to continue growing once they reach the minimum reproductive size is required to reproduce the empirical observation that trout at many sites grow much larger than the minimum for spawning in their species. Second, there are many fitness advantages to continued growth. Larger fish are better able to compete for better feeding and hiding locations. Maintaining high energy reserves reduces the risk of starvation during periods of poor growth conditions. Reproductive success (especially for females) also is likely to increase with size. Fecundity increases sharply with size: *inSTREAM* assumes an exponential increase in the number of eggs produced by a spawner as length increases. Larger females can bury their eggs deeper, reducing their risk of being scoured by high flows. Larger males can compete better for females. (There may be some fitness disadvantages to continued growth. Obviously, one is the additional risk of predation mortality assumed during feeding. Large fish need more food to avoid starvation, potentially making them more vulnerable during prolonged periods of poor growth. And large fish may not be able to hide as completely, or in as many sites, as smaller fish.)

In designing the length function, we made several assumptions. First, the fitness benefits of growth are largely a matter of competition: for a trout, being larger is better in general, but being larger than the other trout is especially important because the ability to compete for food and hiding cover increases with size. A 30-cm trout that is the largest in its population might have higher fitness than a 40-cm trout surrounded by 50-cm competitors. Therefore, the function should be based on a fish's length with respect to the length of its competitors. Second, however, is that the function should encourage fish to grow beyond the size of the largest competitor. If no fish grow beyond the length of the largest fish in the population, the maximum length of the population will decrease as the largest fish successively die. Our third assumption is that the function should encourage large trout to keep growing, but not at a high cost in reduced survival. We do not expect, for example, adult trout to reduce their monthly survival probability by 5-10% in order to continue growing.

A review of the state-variable modeling literature did not reveal any fitness measures that could be adapted for the expected length function. This literature (e.g., Mangel and Clark 1988) typically uses some reproductive event to define the end of a time horizon, with the fitness measure depending on the probability of surviving until the reproductive event and the fecundity at reproduction (a function of size). However, our model uses a constant 90-day time horizon instead of the time until the next spawning season. (We attempted to use the next spawning season as the end of the time horizon, but that attempted did not work because the fish made the assumption that current conditions—food intake, growth, risk—are constant over the time horizon, and over time horizons longer than the 90 days we now use, this assumption is so inaccurate that it leads to unrealistic decisions.)

Considering these factors (and after testing a variety of alternatives), we assumed an expected length function that is a logistic curve defined by two points: the function equals 0.7 at the minimize length needed for reproduction (the parameter *fishSpawnMinLength*) and equals 0.9 at the length of the largest fish currently in the population (Figure 8). This function assumes that all fish "know" the size of the biggest fish in the population, which is inaccurate but a reasonable approximation. Each fish could only know the size of other nearby fish, but we expect the largest fish in the whole population to be a useful approximation of the largest fish that any individual must compete against. (This approximation is less accurate if there is a very small number of very large fish.)

The expected length function is not very sensitive to the length of the largest fish as long as the largest fish is sufficiently larger than *fishSpawnMinLength* (Figure 8). However, as the largest fish's length decreases toward *fishSpawnMinLength*, the expected length function gets steeper. This means that the expected fitness of small fish increases more rapidly with size when the small fish are competing against only other smaller fish.
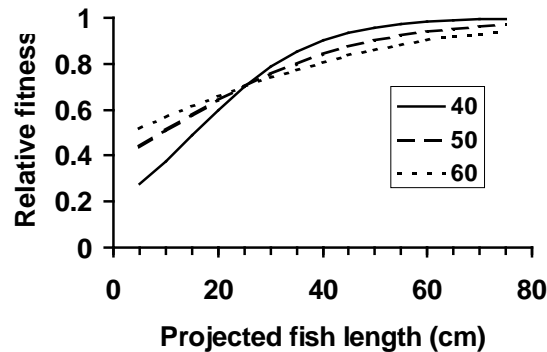
Figure 8. Expected length function for the habitat and activity selection fitness measure. The minimum spawning length is 25 cm and curves are shown for three values of the length of the largest fish: 40, 50, and 60 cm.

When the length of the largest fish gets too close to *fishSpawnMinLength* the expected length function takes on undesirable characteristics, especially extreme steepness for small fish. Therefore, we limit the function by requiring its relative fitness (Y) value of 0.9 to be at a length at least 1.5 times *fishSpawnMinLength*. In other words, if the largest fish in the population is only 35 cm long and the value of *fishSpawnMinLength* is 25 cm, then the expected length function is defined to be 0.7 at 25 cm and 0.9 at 37.5 cm (1.5 × 25). (This function and its limit are hardcoded in the software, not controlled by parameters.)

This length function of the fitness measure is updated once per day at midnight. Separate functions are used for each trout species, using the species' value of *fishSpawnMinLength*. However, the largest trout of any species is used to define the point where relative fitness is 0.9.

5.2.5.3 Time horizon

The time horizon variable *fishFitnessHorizon* is the number of days over which the terms of the expected maturity 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 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 *expectedMaturity*—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 *expectedMaturity* 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 *expectedMaturity* to vary almost exclusively with growth rates when growth was less than the minimum needed to maintain a condition factor of 1.0.

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There is little literature addressing the issue of fitness time horizons but two studies are relevant. Bull et al. (1996) used a decision-making model similar to habitat selection in *inSTREAM* and assumed overwintering juvenile salmon used the remaining winter period as a time horizon. Thorpe et al. (1998) proposed using the duration of various salmonid life stages as time horizons. Following the lead of this literature and assuming that fish anticipate seasonal changes in habitat conditions and their life stage, it makes sense to assume they use a habitat selection time horizon of several months. Another reason to use a time horizon of several months is that it can take that long for the fitness consequences of underfeeding—starvation—to take effect (Section 5.4.6).

An analysis of the sensitivity of *inSTREAM* 4.2 to the value of *fishFitnessHorizon* (Railsback et al. 2009) shows that population success, evaluated as mean adult trout biomass, was relatively insensitive to the value of *fishFitnessHorizon*, being high over a range of about 70 to 120 d. Considering the strong evolutionary pressure for trout to make good habitat selection decisions, it seems appropriate to use values of *fishFitnessHorizon* that result in high population success. Most applications of *inSTREAM* to date have used a value of 90 d.

5.3 Feeding and Growth

5.3.1 Overview

This section describes the methods for determining the growth—change in weight and length—that fish obtain in their habitat cells. These methods are used both in the habitat and activity selection decision to determine how much growth a fish would obtain in each cell it considers as a potential destination, and to simulate growth (one of the actions fish execute each model step; Section 2.3). This first subsection provides an overview of the feeding and growth methods, listing the major assumptions. Full detail is provided starting with Section 5.3.2.

In *inSTREAM-SD*, each fish's growth is calculated for each time step. Hourly growth is calculated using hourly rates (food intake, metabolic demand, etc.) and then multiplied by the length (in hours) of the time step.

The feeding and growth formulation of *inSTREAM* 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 way that *inSTREAM* is different from previous feeding and growth models 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 4.2.4).

inSTREAM does not specify the exact kinds of food consumed by fish, but its feeding formulation and parameters generally represent invertebrate food. Even though the model assumes small fish are vulnerable to predation by adult trout (Section 5.4.4), fish generally do not make up a large part of the diet of stream trout. Therefore, piscivory is not represented in the feeding methods.

Fish in *inSTREAM* 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 *inSTREAM* 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.

In *inSTREAM-SD*, hiding is added as an alternative to feeding. The same methods for calculating growth are used for fish that are hiding. Hiding fish are simply assumed to have zero food intake and zero energy cost of swimming. Growth is therefore always negative for hiding.

From a fish's growth, its length and condition factor are updated. How an organism allocates its energy intake to growth (increase in length), storage (increase or decrease 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, *inSTREAM* 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 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 *inSTREAM* (*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.

- If the resulting new weight is greater than *fishHealthyWeight* calculated for the fish's current length, the fish grows in length. Its condition is set to 1.0, *fishHealthyWeight* is set to its new weight, and its length is updated:

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

- If instead the resulting new weight is less than *fishHealthyWeight*, the fish's condition is less than 1.0 so length does not increase. Condition is updated as *fishWeight* over *fishHealthyWeight*.

This formulation is simple and succeeds in producing reasonably realistic patterns of trout 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 time steps when 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 step of negative net energy intake (e.g., from hiding) 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 5.4.6).

- This weight-based condition factor is not the best predictor of starvation mortality (Section 5.4.6).

- 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, *inSTREAM* cannot predict the existence of unusually fat fish.

- The energetics of reproduction are not considered. While *inSTREAM* does simulate weight loss due to spawning (Section 5.1.5), it does not model storage of energy for gonad development and how gonad production affects length and weight.

These limitations could be eliminated only by making *inSTREAM* 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 *inSTREAM*'s objectives.

Example parameter values for the length-weight relationship are provided in Table 9. These parameters should not simply be regression parameters calculated from observed data; they

must describe a site-specific length-weight relation for fish <u>in good condition</u>. Methods for developing the parameters are discussed in Section 16.8 of Railsback et al. (2009).

Table 9— Example parameter values for the length-weight relation, for length in cm and weight in g.

Species and site	Parameter	Value
Cutthroat trout, Little Jones Creek, Del Norte County, California (Railsback and Harvey 2001)	*fishWeightParamA*	0.0124
	fishWeightParamB	2.98
Rainbow trout, Tule River, Tulare County, California (Van Winkle et al. 1996)	*fishWeightParamA*	0.0134
	fishWeightParamB	2.96
Brown trout, Tule River, Tulare County, California (Van Winkle et al. 1996)	*fishWeightParamA*	0.0123
	fishWeightParamB	2.97

5.3.2 Activity budget and feeding penalty for movement

Energy intake and costs differ between feeding vs. resting fish. Energetic calculations are based on hourly energy rates (j/h), so energy totals for a time step are simply the hourly rates multiplied by how many hours long the time step is.

Some previous versions of *inSTREAM* assumed that no feeding occurs when the temperature is less than parameter *fishMinFeedTemp*, but this assumption has been removed because it caused unrealistic prolonged weight loss during cold periods.

A major purpose of *inSTREAM-SD* is to evaluate effects of multiple, rapid, changes in flow within a day. One of the mechanisms that has been suggested as an effect of rapid flow variation on fish is that moving in response to flow changes disrupts feeding. To simulate this mechanism, *inSTREAM-SD* includes a penalty to food energy intake for fish that move. We assume that if a fish moves to a different cell at any model step, it foregoes the amount of food it would have received during the time period specified by parameter *fishMovePenaltyTime* (h). Furthermore, the fish is assumed to swim at the cell's mean water velocity during the penalty time, without benefit of velocity shelter (if the trout is drift-feeding) or hiding cover (if the trout is hiding). The total net energy intake for a trout during a time step is equal to (1) the negative net energy intake during the penalty time, plus (2) the trout's hourly net energy intake rate for its cell and activity multiplied by (time step length minus *fishMovePenaltyTime*). This penalty is assumed *not* to be considered by the fish when deciding whether to move; the alternative assumption that trout do consider the movement penalty would provide a small disincentive to movement.

Values for *fishMovePenaltyTime* must be equal to or greater than zero, and the food intake penalty is limited so it cannot exceed food intake during a time step. (For example, if *fishMovePenaltyTime* were set to 2 h, the food intake during a one-hour model step would be zero, not negative.)

There is as yet no reliable empirical basis for a value of *fishMovePenaltyTime*. As a conservative guess, 0.25 h is used as a baseline value.

5.3.3 Food intake: drift feeding strategy

Drift feeding fish wait and capture invertebrates as they are carried within range by the current. Version 6 modifies the drift feeding energy intake formulation of *inSTREAM* 4.2, which is unique but conceptually related to the previous feeding and net energy intake models cited in Section 5.3.1. This literature shows clearly that the distance over which fish can see and capture food increases with trout size and decreases with water velocity. Unlike previous models, *inSTREAM* includes the negative effect of turbidity on the ability of trout to see and capture prey. Turbidity can vary dramatically among sites and over time, and its effects on trout feeding are strong and relatively predictable. Unlike some previous models of drift feeding, *inSTREAM* 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. This method is also unique in representing the difference in feeding success between daytime and night.

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 with dimensions that 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 4.1.1) 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), the size of the prey (bigger prey being easier to detect), and light levels. 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 9). 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 9 was chosen for several reasons. First, it captures the fact that very small trout cannot use as wide a range of prey sizes as larger trout can, a process not otherwise represented in the feeding model. Second, a logarithmic fit to these data predicts negative detection distances for trout 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*,

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defined below). The pre-calibration analysis indicated that the growth rates of very small trout are very sensitive to the intercept. An intercept of 4.0 was found to provide growth of very small trout that was realistic at the same drift food availability values that produce realistic growth rates in larger trout.
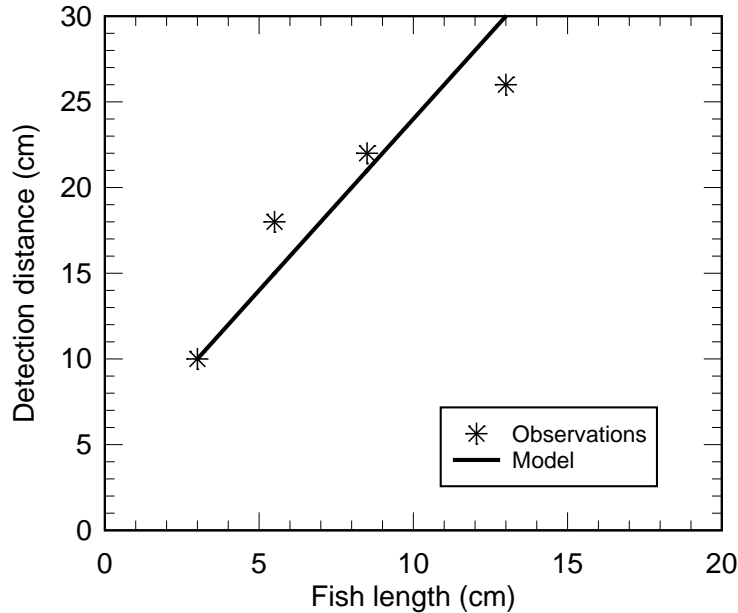
Figure 9. Relation between fish length and prey detection distance observed by Schmidt and O'Brien (1982), for arctic grayling feeding on 0.2 cm zooplankton.

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 *inSTREAM* 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, *inSTREAM* 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 shows a clear effect of turbidity at levels below 5 NTUs (see, e.g., Figure 10), and it seems likely that below such a threshold

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reactive distance is limited by other factors such as turbulence and the ability to (or net benefit of) catching food items very far away. Another reason for assuming a turbidity threshold is to avoid making *inSTREAM* 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, *inSTREAM* includes a parameter *fishTurbidMin* which limits the effect of turbidity on detection distance (Figure 10).
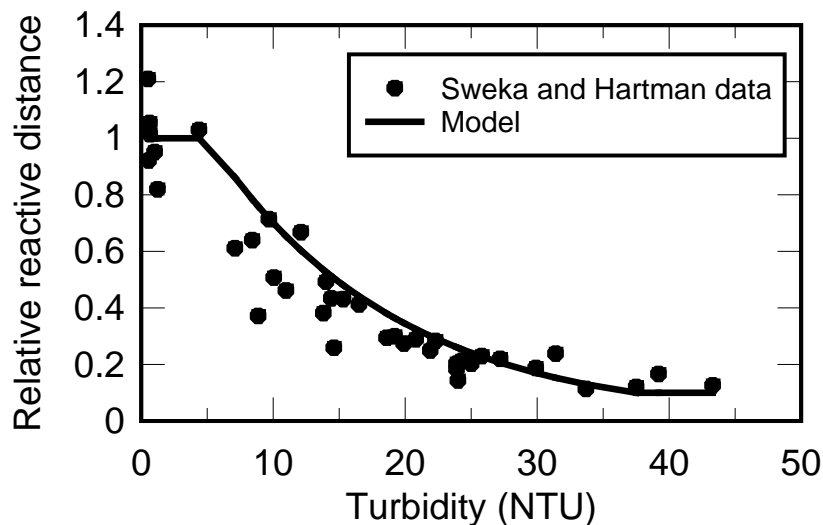
Figure 10. Relative detection distance vs. turbidity: model and data of Sweka and Hartman (2001) used to fit the model.

The difference between day and night in light levels is represented in *inSTREAM-SD* simply by multiplying detection distance by a parameter *fishDetectDistNightFactor* when feeding is at night.

The value of *fishDetectDistNightFactor* was determined from literature and tested during calibration. The relative ability of salmonids to see and capture food during daytime vs. night was studied by Fraser and Metcalfe (1997) and reviewed by Metcalfe et al. (1999). This literature does not provide a strong quantitative basis for modeling the effect of light level on feeding, but concluded that at night juvenile salmonids are, at light levels typical of overcast to clear skies and a shaded stream, between 10 and 35% as efficient at capturing drifting prey as they are during the day. Schmidt and O'Brien (1982) measured detection distance in Arctic grayling feeding on large zooplankton at various light levels. Schmidt and O'Brien found that night detection distances were 20-33% of daytime levels, but the zooplankton they used were relatively small and transparent. This parameter could vary among sites due to factors like cloud cover and topography. A value of 0.5 for *fishReactDistNightFactor* reduces feeding to 25% of daytime values.

(Note that this formulation reduces the incentive for fish to use deeper water at night. The area of stream cross-section over which fish capture drift food is limited vertically by the minimum of the depth and the reactive distance; if the depth exceeds the reactive distance, there is no food intake benefit to using deeper water.)

Detection distance is therefore modeled with this equation:

$$detectDistance = lengthFunction \times turbidityFunction \times lightFunction$$

where:

lengthFunction = *fishDetectDistParamA* + (*fishDetectDistParamB×fishLength)*

turbidityFunction = 1.0 if *habTurbidity <= fishTurbidThreshold*

   else *turbidityFunction* =

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

lightFunction = 1.0 during daytime and = *fishDectDistNightFactor* during night.

Parameter values are in Table 10. 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.

The drift capture area is calculated from detection distance. Several previous trout 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. *inSTREAM* 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 trout 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 *inSTREAM* (Figure 9). 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 *inSTREAM*, 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 11). (Maximum sustainable swimming speed is a function of fish length and water temperature. The method for modeling it is presented in Section 5.4.2.) 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.

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

Parameters for this logistic function are in Table 10.
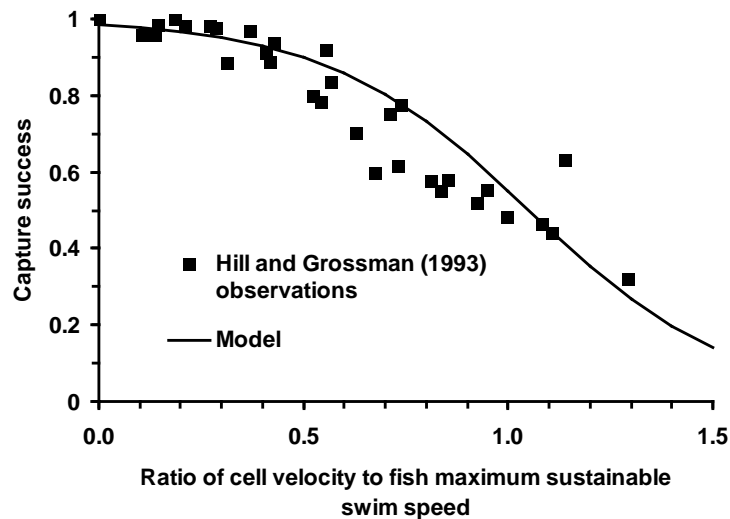
Figure 11. Capture success model and the laboratory observations it was based on.

Table 10. 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
fishDetectDist NightFactor	Factor by which detection distance is multiplied at night (unitless, 0.0-1.0)	0.5

Sensitivity of the drift feeding model to velocity and fish size are explored in Section 5.3.10.

5.3.4 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 trout. 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, *inSTREAM* 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 5.3.7.)

To represent the effect of night on search feeding, we simply apply a constant factor, the fish parameter *fishSearchNightFactor* (unitless, with value between zero and one), that reduces search feeding intake at night. Using the same literature cited above for drift feeding, we selected a value of 0.5 for this parameter and then tested it during calibration.

The search food intake model is:

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

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 4.2.4), *fishMaxSwimSpeed* is the fish's maximum sustainable swimming speed (cm/s; Section 5.4.2), 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. The value of *nightEffect* is 1.0 during daytime and equal to *fishSearchNightFactor* at night.

There is an important difference between *fishSearchNightFactor* and the similar parameter for drift feeding, *fishReactDistNightFactor*. Food intake increases linearly with the value of *fishSearchNightFactor* but increases with the square of *fishReactDistNightFactor* (unless the depth is less than the reactive distance). Therefore, a value of 0.5 for *fishSearchNightFactor* reduces search intake by 50% but a value of 0.5 for *fishReactDistNightFactor* reduces drift intake by 75%.

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, our experiments (Harvey and White 2008) show that trout can continue feeding successfully on benthic food at relatively high turbidities. 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 *inSTREAM*.

5.3.5 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. 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.

5.3.5.1 Maximum consumption as a daily rate

This maximum consumption rate is different from other feeding and growth rates modeled in *inSTREAM-SD* in being time-scale dependent: the maximum rate at which a fish can consume food over an hour is different from maximum consumption over a day. A fish can fill its gut rapidly over a short time, but then it takes many hours of digestion to empty the gut again. A fish can obtain a full day's food consumption by feeding during only part of a day. Therefore, *cMax* is modeled as a daily, not hourly, rate.

We consider *cMax* in the fishs' habitat and activity selection process in this way. When a fish calculates the food intake it would get from either drift (Section 5.3.3) or search feeding (Section 5.3.4), when either evaluating cells as feeding destination or calculating daily growth in the cell they do feed ing, the fish checks whether its total food intake for a full day—the sum of its actual intake for the day (starting at first hour of daylight) and the intake for the cell currently being considered—is less or equal to than *cMax*. The value of *cMax* is updated for each cell the fish considers because (being temperature-dependent) it can vary among cells if the cells are in different reaches. (This means that a fish's value of *cMax* varies within a day as its weight changes.) If the full day's intake is greater than *cMax*, then the net energy intake for the full day is reduced to the level it would be if intake was equal to *cMax*. The total net energy is reduced by the amount *(total intake - cMax) * habPreyEnergyDensity*. Because *cMax* varies within a day with fish weight, it is possible for the amount *(total intake - cMax)* to be negative, in which case intake is set to zero.

Actual food consumption is limited by *cMax* during the growth method in this way:

- The fish keep track of their total consumption in a full day. At the start of the daytime phase, the fish instance variable *fishActualDailyIntake* is set to zero.
- During the "grow" action at the start of each model step, each fish's value of *fishActualDailyIntake* is incremented by the food intake (g) it obtained the previous step.
- When a model trout tells its chosen habitat cell how much food it consumed (so the cell can track how much food remains available for smaller trout) this consumption value includes any limitation of intake by *cMax*.

5.3.5.1 Maximum daily consumption model

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 *inSTREAM* 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 11) 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 *inSTREAM* 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 12).
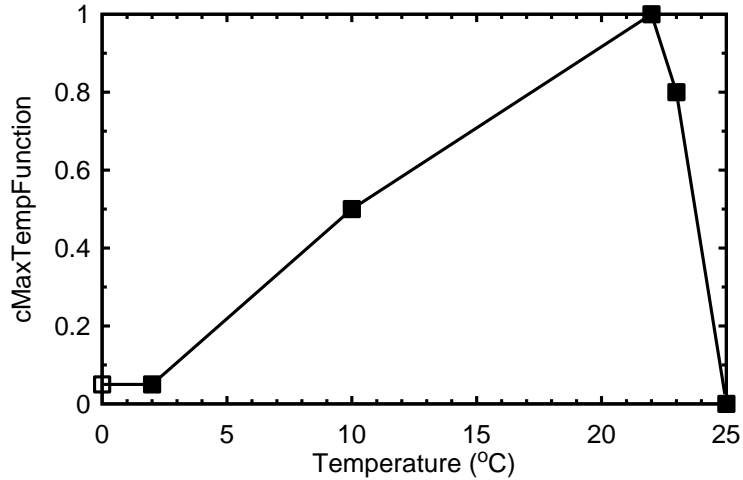
Figure 12. Temperature function for *cMax*.

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 *inSTREAM*, the parameters in Table 11 and Table 12 are cautiously recommended for all stream trout species.

Table 11. 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 12. Parameter values for temperature function of maximum consumption. Each row in the table defines one of the points in Figure 12.

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

5.3.6 Food intake: limitation by food availability

The hourly food intake rate of each fish can be limited by the amount of drift (*driftHourlyCellAvail*, g/h) and search (*searchHourlyCellAvail*, g/h) food available in its cell. These hourly food availability rates are the rate at which food is produced in the cell, minus food consumption by larger fish (Section 4.2.4.2). Therefore, hierarchical competition for food is implemented via the food availability rates. If an hourly food intake rate determined by a fish during feeding simulations (Sections 5.3.3, 5.3.4) exceeds the corresponding (drift, search) food availability rate, it is reduced to that availability rate.

5.3.7 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 *inSTREAM*, 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 trout swim within a time step, 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 the reach 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 *inSTREAM* 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*. An application of *inSTREAM* to the Green River, Utah (Railsback et al. 2005), where substrates are relatively small and embedded, used a value of 0.5.

Velocity shelter access. Model trout 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 4.2.3).

- 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. *inSTREAM* 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. The parameters that Rand et al. (1993) developed for steelhead trout (converted from calories to joules; Table 13) are widely used and appear to be the best available for stream trout in general. In *inSTREAM-SD*, respiration is treated as an hourly rate.

This formulation breaks respiration into two parts: standard respiration (*respStandard*, j/h) takes place 24 h/d and includes no effect of activity; activity respiration (*respActivity*, j/h) is the energy needed to swim during feeding. Total respiration (*respTotal*, j/h) is the sum of these two. The equations are:

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

$$respStandard = \frac{\left(fishRespParamA \times fishWeight^{fishRespParamB} \right) \times \exp\left(fishRespParamC \times temperature \right)}{24} \, ,$$

and

$$respActivity = \left[\exp\left(fishRespParamD \times swimSpeed \right) - 1 \right] \times respStandard \, .$$

When fish are hiding, *swimSpeed* is assumed zero and hence *respActivity* is zero. 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 13. 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*.

5.3.8 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 *inSTREAM* 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, *inSTREAM* uses the *cMax* function to limit food consumption at extreme temperatures.

5.3.9 Feeding strategy selection, net energy benefits, and growth

The feeding strategy selection, net energy, and growth methods calculate a fish's hourly growth for a specific habitat cell and activity. 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 *inSTREAM*. The literature summarized by Hanson et al. (1997) indicates that 5900 j/g is a reasonable value for all stream trout.

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, searchIntake*) calculated using the methods described above.

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

    hourlyPotentialDriftFood = driftIntake × feedTime.

2. Calculate the actual drift intake rate *hourlyDriftFoodIntake* (g/h), considering whether it is limited by actual food availability (as described in Section 5.3.6) or by the physiological maximum intake, *cMax* (using the method described at Section 5.3.5).

3. Convert hourly drift intake in grams of food to joules of energy, *hourlyDriftEnergyIntake* (j/h):

    hourlyDriftEnergyIntake = hourlyDriftFoodIntake × habPreyEnergyDensity.

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

    hourlyDriftNetEnergy = hourlyDriftEnergyIntake - respTotal.

5. Determine the hourly search feeding intake that would be obtained in the absence of more dominant fish in the cell, *hourlyPotentialSearchFood* (g/h):

    hourlyPotentialSearchFood = searchIntake × feedTime.

6. Calculate the actual search intake *hourlySearchFoodIntake* (g/h), considering whether it is limited by food availability (Section 5.3.6) or maximum daily intake (Section 5.3.5).

7. Convert hourly search intake to joules of energy, *hourlySearchEnergyIntake* (j/h):

    hourlySearchEnergyIntake = hourlySearchFoodIntake × habPreyEnergyDensity.

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

    hourlySearchNetEnergy = hourlySearchEnergyIntake - respTotal.

9. Select the most profitable feeding strategy by comparing *hourlyDriftNetEnergy* to *hourlySearchNetEnergy*; and determine the energy intake for the best strategy:

    bestNetEnergy = max(*hourlyDriftNetEnergy, hourlySearchNetEnergy*).

10. Convert net energy intake to hourly growth *hourlyGrowth* (g/h):

    hourlyGrowth = bestNetEnergy / fishEnergyDensity.

11. Update the fish's weight, considering the length of the time step being simulated:

$$fishWeight = fishWeight + (hourlyGrowth \times numHoursSinceLastStep).$$

In the final step, *fishWeight* is set to zero if its calculated value is negative. (Negative weight can result when small fish calculate growth for cells where swimming speed would be extremely high.)

For calculating a fish's growth at the end of a time step (not for determining hourly growth rate for the habitat and activity selection decision), the final step in this process is modified as described in Section 5.3.2 to include the effects of a "feeding penalty" if the fish moved to a different cell at the start of the time step.

5.3.10 Preliminary parameter estimation for feeding and growth

There are many variables affecting growth so it must be calibrated incrementally. This section identifies ranges of values for the food production parameters that produce reasonable feeding and growth rates under simplified conditions. This preliminary parameter estimation makes it easier to calibrate growth in the whole model, where habitat selection and competition are additional processes that strongly affect growth.

(This section discusses calibration of growth by adjusting the parameters for food production. The key food parameter, *habDriftConc*, can in fact be measured in the field instead of calibrated. However, attempting to use measured drift concentrations is actually discouraged for several reasons. First, this parameter captures many of the uncertainties resulting from model simplifications such as ignoring variation in prey size and assuming fish feed only during daytime; hence, even an accurately measured drift concentration may not produce accurate model results. Second, drift concentration measurements are expensive and uncertain; resources for field studies are probably better spent on fish data to calibrate the model against.)

Reasonable values of the search and drift food availability parameters are found by identifying ranges that meet criteria developed from field observations and laboratory growth data. These criteria are:

- Daily food intake under summer conditions should be in the range of 20 percent to 50 percent of *cMax*. *cMax* should rarely if ever limit food intake. This criterion is based on field research in which <u>average</u> food intake was estimated from observed growth and bioenergetics models. Railsback and Rose (1999), using a bioenergetics formulation similar to that used in *inSTREAM*, found food consumption by trout in relatively small streams of California's Sierra Nevada to average 30–35 percent of *cMax*. At these sites, temperatures were 15-19ºC; *cMax* increases sharply with temperature in this range. Individual fish in excellent habitat could have food intake well above the average. (This criterion may not be valid in unusual situations where food is extremely abundant and trout growth rates very high, or at very low temperatures where *cMax* is very low.)

- Drift feeding should be more profitable than active search feeding, except at low velocities, when turbidity is high, when benthic prey are extremely abundant, or for very small trout. Trout are rarely observed feeding only with the search strategy, and where both strategies are available drift feeding is probably more often preferred (Nielsen 1992; Nislow et al. 1998).

- Growth under good conditions (high food intake, low swimming velocity) should not exceed growth rates observed in lab studies where fish were fed as much as they could eat (e.g., Myrick 1998, Myrick and Cech 2000). These lab growth rates are in the range of 2-6 percent of body weight per day, varying with temperature.

To estimate food parameter values, the entire feeding and growth formulation of *inSTREAM* was implemented in a spreadsheet. Parameter values from Table 10, Table 11, Table 12, and Table 13 were used. Summer conditions were represented: *feedTime* = 16 h and temperature = 15ºC. Turbidity was assumed to be zero. Both juvenile (5 cm length; 1.5 g weight) and adult (15 cm, 40 g) trout were simulated.

Reasonable values for the drift food parameter *habDriftConc* were identified as the range producing food intake (g/d) of 20–50 percent of *cMax* in the adult trout, for trout using near-optimal velocities and velocity shelter. This range is $5×10^{-10}$ to $12×10^{-10}$ g/cm^3. Within this range of *habDriftConc*, adult trout growth ranged between 0.5 and 2.5 percent body weight per day, reasonable rates. For 5 cm juvenile trout, this range of *habDriftConc* produced food intake between 50 and 100 percent of *cMax* and growth in the range of 5 to 15 percent per day; the lower ends of these ranges are consistent with observed rates.

The value of *habDriftRegenDist* was estimated by assuming a cell that contains 15 cm trout, each trout having a square territory 150 cm on each side. This assumption is based on the observations collected by Grant and Kramer (1990), which indicate that 15 cm trout have an average territory diameter of 150 cm. The cell is also assumed to have a depth of 30 cm and velocity of 30 cm/s, near-optimal feeding conditions. The trout were assumed to get an intake of 30 percent of *cMax*, or 0.11 g/h, and that under these conditions drift food production exactly equals consumption by the trout. With *habDriftConc* in the range of $5×10^{-10}$ to $7×10^{-10}$ g/cm^3, the value of *habDriftRegenDist* must be approximately 300–500 cm.

The assumptions used to estimate search intake parameters are (a) a search-feeding fish consumes the production of two square meters, so the value of *fishSearchArea* is 20,000 cm^2; and (b) a 5 cm trout can maintain growth of zero to 2 percent body weight per day by search feeding for 16 h/d at 15°, at velocities of 10 cm/s or less. The range of *habSearchProd* values producing this growth range is $2×10^{-7}$ to $5×10^{-7}$ g/cm^2/h.

There are few published estimates of trout food production rates that are comparable to these parameter estimates. Published estimates of invertebrate production do not separate drift from invertebrates eaten at the benthic surface. The rate at which food drops in from overhead (part of food production in *inSTREAM*) is also rarely measured. Poff and Huryn (1998) report overall food production rates in Atlantic salmon streams in the range of 4-24 g dry weight per m^2 per year, which converts to $10 – 60×10^{-7}$ g/cm^2/h (assuming a typical ratio of 20 for dry:wet weight; Hanson et al. 1997). The range of *habSearchProd* estimated above ($2×10^{-7}$ to $5×10^{-7}$ g/cm^2/h) appears reasonable compared to this value: *habSearchProd* is expected to be a relatively small but not negligible fraction of the total production rate.

Examining how food intake and growth vary with cell velocity helps understand the feeding and growth formulation. Figure 13 illustrates how daily food intake (evaluated as the percent of *cMax*) varies with velocity, for both 5 cm juveniles and 15 cm adult trout, for both feeding strategies. Figure 14 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 15 is identical to Figure 14 except for depicting winter conditions, with a temperature of 5⁰C and feeding time of 12 h.
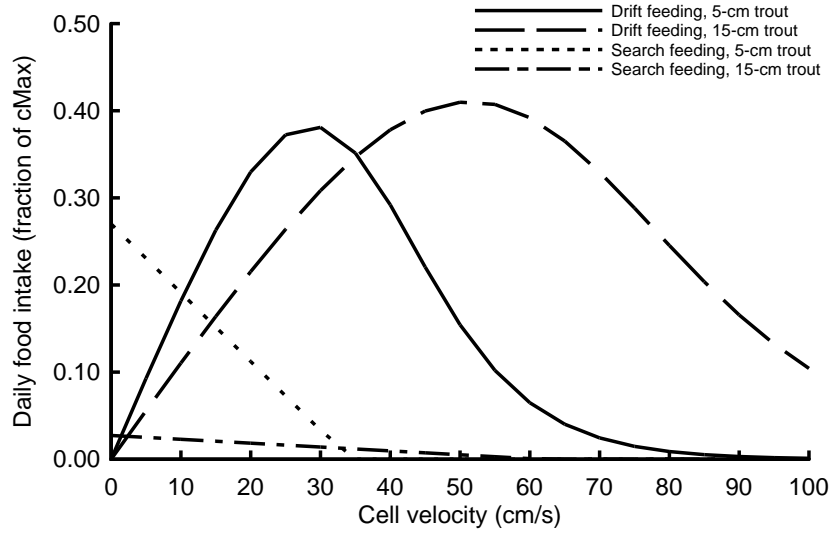
Figure 13. Variation in food intake with velocity for two sizes of trout, using drift or search feeding. Intake is depicted as percent of *cMax* (physiological maximum daily intake).
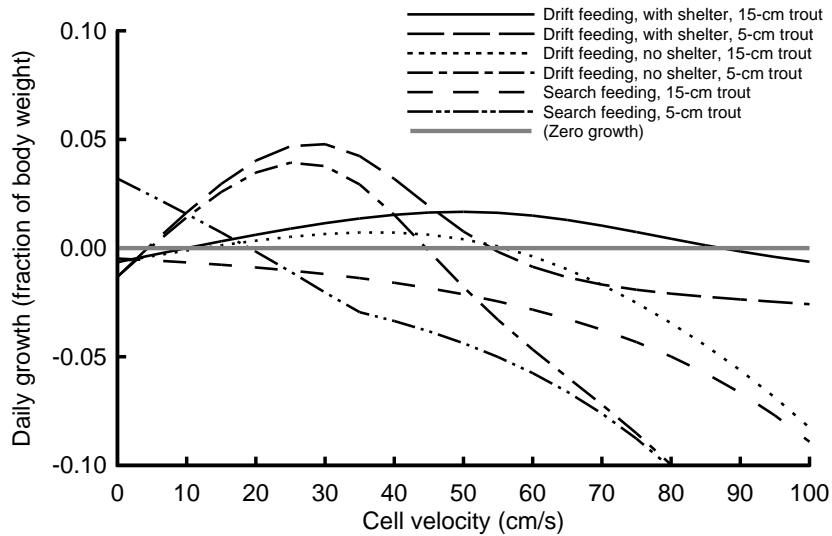
Figure 14. Variation in growth rate with velocity for two sizes of trout, drift and search feeding strategies. Growth is depicted as percent of body mass per day.
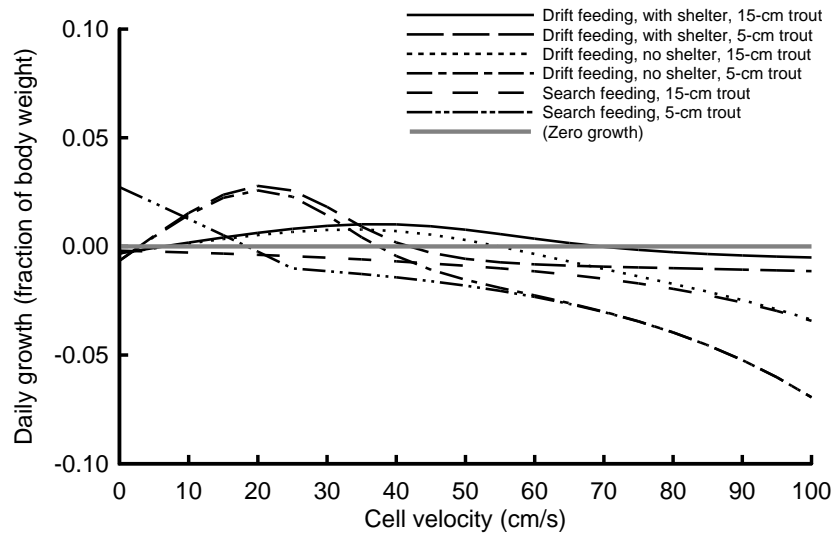
Figure 15. Variation in growth rate with velocity, under winter conditions.

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

- 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.

5.4 Fish Survival

Survival simulations determine, each step, 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 *inSTREAM* as survival probabilities: the daily probability of not being killed by one specific mortality source. The mortality sources in *inSTREAM* 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,

- Predation by fish and,

- In *inSTREAM-SD*, angling.

The primary reason that *inSTREAM* 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 *inSTREAM*—habitat selection—depends on survival probabilities. For habitat selection to be modeled realistically, *inSTREAM* must represent how different mortality sources vary differently over time, among fish, and over space. And, for *inSTREAM-SD* to represent activity selection it is essential to represent how survival varies between day and night and between feeding and hiding.

Survival probabilities are used for two purposes. First, survival probabilities are used during habitat and activity selection (Section 5.2) 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 for mortality are used in modeling habitat and activity selection.

Like other versions, *inSTREAM-SD* models mortality using daily survival probabilities, but calculates survival each sub-daily model step. A potentially important implicit assumption is therefore that survival probabilities are not timescale-dependent. Survival probabilities are timescale-dependent if survival probability is non-linear with respect to the duration of exposure to risk. Predation risk is assumed to result from predator-prey encounters that occur over a few seconds or minutes, so the risk of being captured by a predator in two hours can be modeled as twice the risk of being captured in one hour and predation can be assumed *not* timescale-dependent. In contrast, the thermal stress risk to a trout exposed to a temperature of 26° may be negligible over one hour, but high over a full day (due to biochemical changes that become irreversible over several hours). High temperature mortality is therefore likely to be timescale-dependent, but *inSTREAM-SD* assumes temperature varies daily, not hourly.

Survival of each fish is simulated each model step to determine if the fish survived the preceding time step. To adjust each daily survival probability for the time step length, we simply raise the probability to the power: *numHoursSinceLastStep* / 24.

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. At each model step, 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 and from the length of the preceding time step.

- 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 is assumed to have died during the previous time step 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.

The order in which mortality sources are evaluated can have a (usually 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 2.3.

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 short times. 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. The two predation formulations differ from other versions of *inSTREAM* in explicitly representing the difference in survival between day and night and representing competition for hiding cover.

5.4.1 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 *inSTREAM* 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 trout 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 14 (illustrated in Figure 16) appear suitable for sites with relatively low diurnal variation in temperature; they produce survival survival of 0.98 at 24°, 0.88 at 26°, and < 0.5 at 28°.
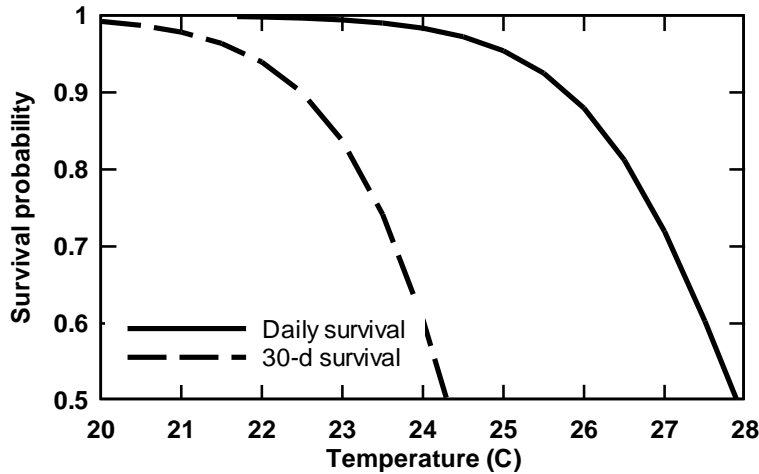
Figure 16. Survival probability function for high temperature. Daily survival (solid line) is the probability of a trout surviving high temperature mortality for one day. 30-d survival (dashed line) is the probability for surviving the temperature for 30 days (equal to the daily survival raised to the power 30).

Table 14. Parameter values for high temperature mortality.

Parameter	Definition	Value
mortFishHiTT9	Daily mean temperature (°C) at which high temperature survival is 90 pct	25.8
mortFishHiTT1	Daily mean temperature (°C) at which high temperature survival is 10 pct	30

5.4.2 High velocity

The high velocity survival function represents the potential for trout to suffer fatigue or lose their ability to hold position in a cell with high velocity. This function is included not because trout 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 5.3.7): 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*. In *inSTREAM-SD*, fish can also use hiding cover; a algorithm explained below is used to estimate their exposure to high velocity risk.

Maximum sustainable swim speed (*maxSwimSpeed*, cm/s) is a particularly important state variable for model trout. As a component of both high velocity mortality and drift feeding (Section 5.3.3), *maxSwimSpeed* strongly affects the relationship between a cell's velocity and habitat quality for various size trout. Because *inSTREAM* uses multi-hour time steps, 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 trout 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 trout 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 17). Second, *maxSwimSpeed* varies nonlinearly with temperature, peaking at temperatures around 10-15º (Figure 18). 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 15. 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 trout length (parameters *fishMaxSwimParamA* and *fishMaxSwimParamB*) was fit using observations made at temperatures between 10 and 15ºC (Figure 17). 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 15⁰ in the same study, vs. (b) temperature (Figure 18).
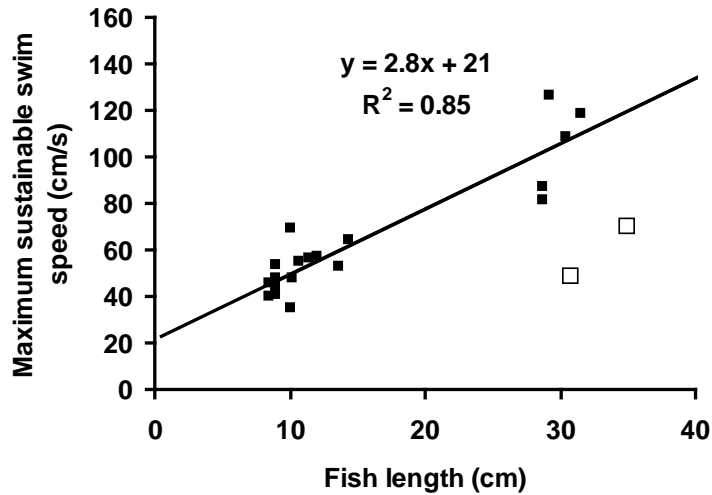
Figure 17. Maximum sustainable swimming speed as a function of fish length; measurements made at 10-15⁰ C. The points marked as open squares were omitted as outliers.
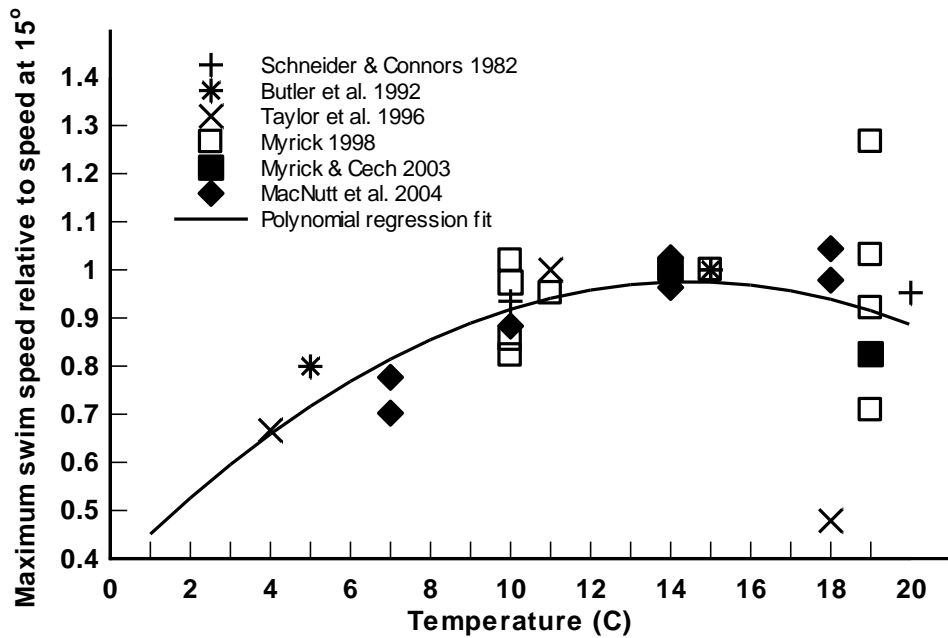
Figure 18. Variation in maximum sustainable swim speed with temperature. Observations from four studies are shown separately. The Y axis is the measured swim speed divided by the speed measured at (or near) 15⁰ in the same study.

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 19). The parameters for this function (Table 15) 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 trout can often use to reduce swimming effort in natural conditions, and (b) stream fish are likely to be in better condition than laboratory fish.
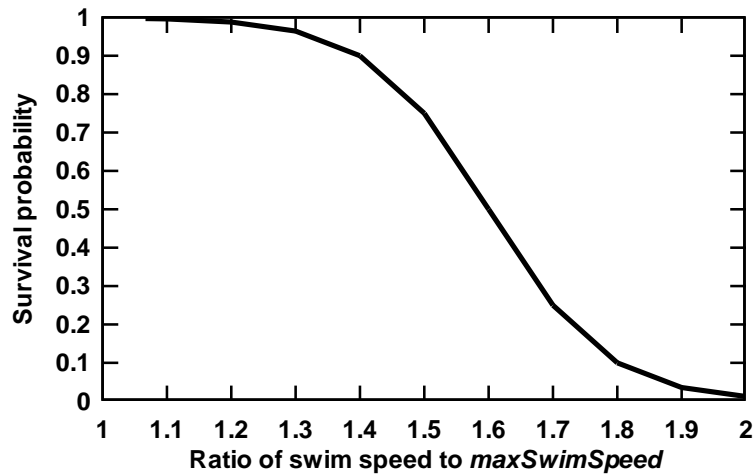
Figure 19. Survival probability function for high velocity. The X axis is the fish's actual swimming speed divided by its maximum sustainable swimming speed.

Finally, for fish using hiding cover the survival probability is increased by an amount controlled by the parameter *mortFishVelocityCoverFactor* (unitless). This adjustment is made because fish in hiding cover are typically highly sheltered from water column velocities, but during extreme velocities shelter may collapse and expose fish to risk. This parameter is the fraction by which high velocity risk is reduced when a fish is in hiding cover. (The survival probability is adjusted by adding to it the value of *mortFishVelocityCoverFactor* times 1.0 minus the pre-adjustment value of high velocity survival.) Hence, if *mortFishVelocityCoverFactor* is 0.75 and high velocity survival is 0.99 for fish not in hiding cover, survival for fish using hiding cover is 0.9975. The value of *mortFishVelocityCoverFactor* should be evaluated for each study site, especially considering what kind of hiding cover is available and how much protection it provides against extreme velocities (e.g., large boulders may justify a value near 1.0 whereas vegetation as cover may justify a much lower value).

Table 15. 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 ($^{\circ}C^{-2}$)	-0.0029
fishMaxSwimParamD	Temperature coefficient in maximum swim speed equation ($^{\circ}C^{-1}$)	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
mortFishVelocityCover Factor	Fraction by which risk of high-velocity mortality is reduced for fish using hiding cover (unitless; 0-1)	0.75

5.4.3 Stranding and shallow habitat

Stranding and shallow habitat mortality (referred to as "stranding" in *inSTREAM* documentation and software) represents the risk of using cells that are extremely shallow or dry. This risk arises from two processes: stranding if a fish is unable to leave a cell that becomes dry as flow decreases, and excess predation in dry or extremely shallow habitat.

Most "stranding" mortality in *inSTREAM* occurs in cells with depths just above zero, and so represents the predation process. Fish in *inSTREAM* have strong incentives to avoid cells with near-zero depth: drift food intake and survival of terrestrial predation are low. Fish are not allowed to select, or stay in, dry cells unless no alternatives are available (Section 5.2.2.3). However, in *inSTREAM-SD*, search feeding in shallow, slow habitat at night is profitable for many fish and can lead to stranding mortality. In addition, 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 20; Table 16). 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.
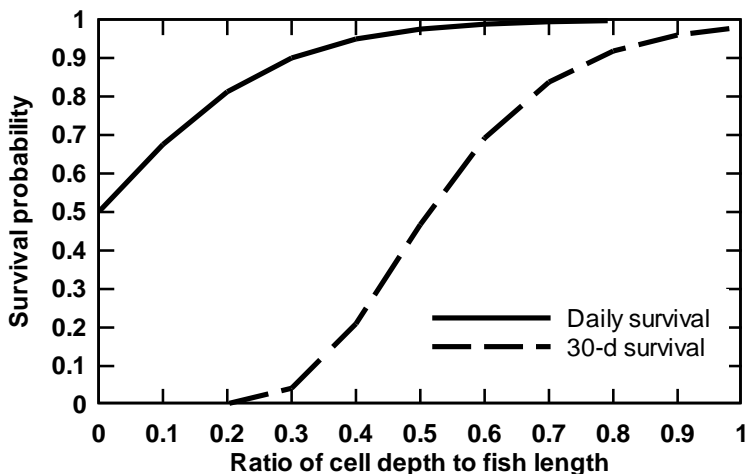
Figure 20. Survival probability function for stranding, showing the probability for surviving one day (solid line) and for 30 days (dashed line).

Table 16. 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

5.4.4 Aquatic predation

The aquatic predation formulation represents mortality due to predation by fish. In many but not all trout populations, the dominant source of aquatic predation is cannibalism by large trout. By adjusting parameter values, the formulation can be made to apply both to sites where the modeled trout are the only piscivorous fish and sites where non-trout fish, not otherwise represented in *inSTREAM*, are a significant risk. The formulation can represent the effect of adult trout density on aquatic predation survival, making this survival probability the only component of *inSTREAM* with <u>direct</u> density dependence.

Especially at sites where trout rarely get larger than 20-30 cm, cannibalism by trout is often rare; e.g., at the Little Jones Creek site fewer than 1 percent of adult fish contained juveniles (Railsback and Harvey 2001). However, the risk of predation appears to be an important factor driving habitat selection (e.g., Brown and Moyle 1991): avoiding predation is likely a key reason why small fish prefer shallow water. If aquatic predation rarely occurs, it is likely because small

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fish avoid it with some success by avoiding risky habitat. Also, there have been anecdotal reports of very high cannibalism rates during fry emergence in some salmonids.

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.

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

where *aqPredSurv* is 24-hour 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 difference between day and night survival is represented in *inSTREAM-SD* by using two separate parameters for *mortFishAqPredMin*: *mortFishAqPredDayMin* and *mortFishAqPredNightMin*. Unlike terrestrial predation, aquatic predation survival can be assumed lower at night. Aquatic predation survival is modeled as lower at night for two reasons. First, bigger fish (predators) have bigger eyes and can see better than small fish at low light levels (Hester 1968, cited by Ware 1978). Second, larger fish, being partially released from terrestrial predation risk at night, tend to use shallower habitats where they are more likely to encounter small trout (Section 5.4.5). If we assume a typical pre-calibration estimate of 0.99 for *mortFishAqPredDayMin* and also estimate that mortality at night is 25% higher than during the daytime, then the value of *mortFishAqPredNightMin* is 0.987.

There is no survival increase function for distance to hiding cover in the aquatic predation formulation. This decision was made because only small trout are usually vulnerable to aquatic predators, and small trout are capable of hiding in many places that do not offer refuge to adult trout (e.g., between relatively small cobbles) and hence are not well represented by the cell variable for distance to hiding cover. However, *inSTREAM-SD* does include use of hiding activity and cover as a survival increase function.

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).

Predator density. This function represents how survival of aquatic predation depends on the density of <u>trout</u> predators. The function allows a type of feedback that is potentially important in regulating trout populations: when adult abundance is greatly reduced, juveniles can safely use a wider range of habitat and, hence, have greater growth and survival to adulthood. It is important to understand that this function represents only the effect of trout included in the model; it does not represent non-trout piscivorous fish. The predator density survival increase function causes the survival increase function to increase as the density of piscivorous trout decreases. Two additional assumptions are needed to implement this function.

First, a definition of piscivorous trout must be assumed. Any trout with length greater than the parameter *fishPiscivoryLength* (cm) is assumed to be a potential predator on smaller trout. This is a simplification, because in reality the larger a fish becomes, the larger prey fish it potentially can consume. Considering observed predator—prey size ratios for salmonids (collected and

reviewed by Keeley and Grant 2001), values in the range of 15-30 cm are reasonable for *fishPiscivoryLength*. This parameter should be considered site specific; trout may be piscivorous only at larger sizes in fertile streams where other prey are abundant (Keeley and Grant 2001).

The second additional assumption is chosing the spatial scale over which trout predation is represented. Predator density could be represented in *inSTREAM* at the cell, reach, or multiple-reach scales. The reach scale is chosen because large, piscivorous trout are likely to foray and attack fish in other cells. Therefore, predator density in this survival increase function is defined as the number of trout in the reach with length greater than *fishPiscivoryLength*, divided by the area (cm^2) of the reach (Section 4.1.1).

Parameters for the logistic decrease in survival with increasing predator density depend on whether the modeled trout are the only piscivorous fish. The parameters illustrated in Figure 21 represent a site where there are no non-trout fish predators. The parameters reflect (a) near-zero risk when there are no piscivorous trout, and (b) a steep decline in survival as predator density exceeds one piscivorous trout per 25 m^2 (250,000 cm^2) of reach area. Post et al. (1998) measured the mortality of tethered juvenile trout due to predation by adult trout in lakes. This study showed the risk to increase exponentially with adult trout density, rising very sharply between 8 and 10 predators per 1000 m^3. This result supports a logistic-like relation between adult trout density and juvenile trout survival probability, but the exact relation is not directly applicable to *inSTREAM* because (a) it was obtained in lakes where cover and other habitat complexities may mediate the effect of predator density, and (b) risks were evaluated over 1 hour periods, whereas *inSTREAM* uses a multi-hour time step.

For sites where fish other than the trout represented in the model pose a piscivory risk, parameter values should be adjusted to reflect the reduced importance of trout to survival of aquatic predation. For example, if a site has a dense population of piscivorous pikeminnow, then trout density may have little effect on survival. In that case, the predator density function should be low and relatively flat (e.g., *mortFishAqPredP9* = -1.0; *mortFishAqPredP1* = 0.001).
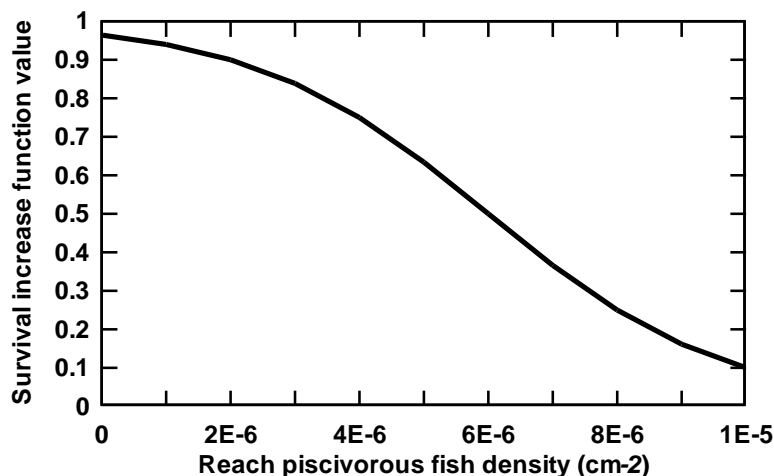
Figure 21. Predator density survival increase function for aquatic predation survival. The X axis is the density (number per cm^2) of piscivorous trout in the fish's reach.

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 22).
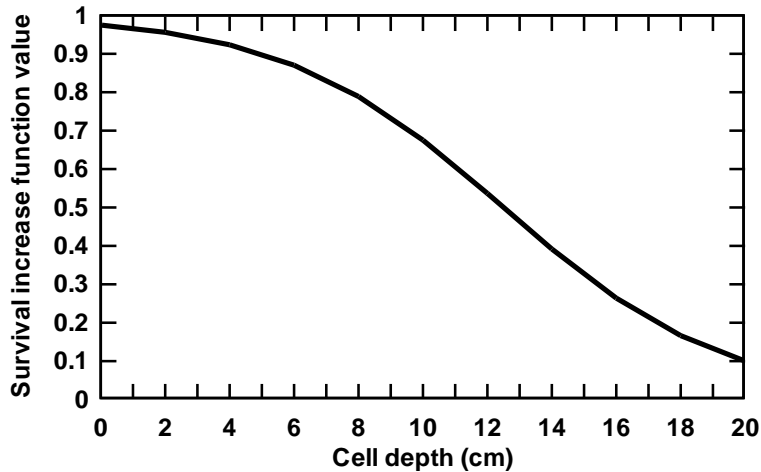
Figure 22. Depth survival increase function for aquatic predation survival.

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 23 illustrates parameters for sites where the only predator fish are trout of 25-30 cm in length. For sites with larger predator fish, the curve should be shifted to the right. For sites such as Little Jones Creek where adult trout are rarely more than 20 cm, survival is likely quite high when length is greater than 8 cm.
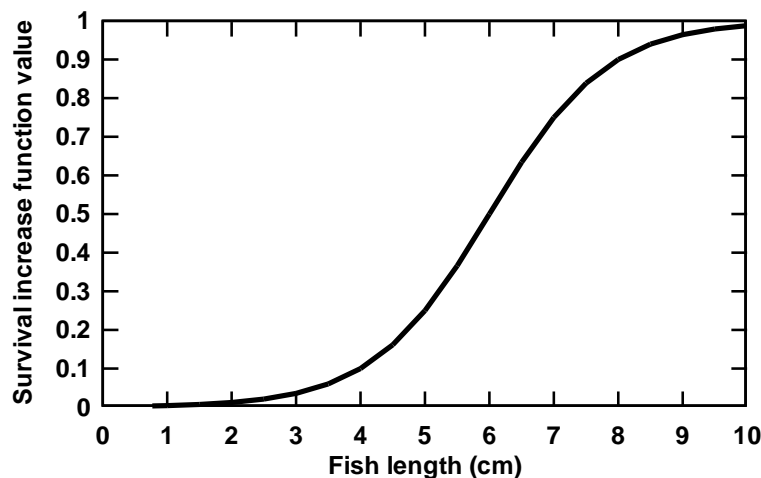
Figure 23. Fish length survival increase function for aquatic predation survival.

Low temperature. This survival increase function reflects how low temperatures reduce the metabolic demands and, therefore, feeding activity of piscivorous fish. The function is based on the bioenergetics of the trout predators, using a decreasing logistic function (Figure 24) that approximates the decline in maximum food consumption (*cMax*) with declining temperature (Section 5.3.5).

The parameters for the low temperature function could be revised if aquatic predation is dominated by non-trout piscivores that do not function as well as trout at low temperatures. Parameter values could be chosen to reflect how metabolic rates and swimming performance of a less cold-adapted predator drops at temperatures below 10°C.
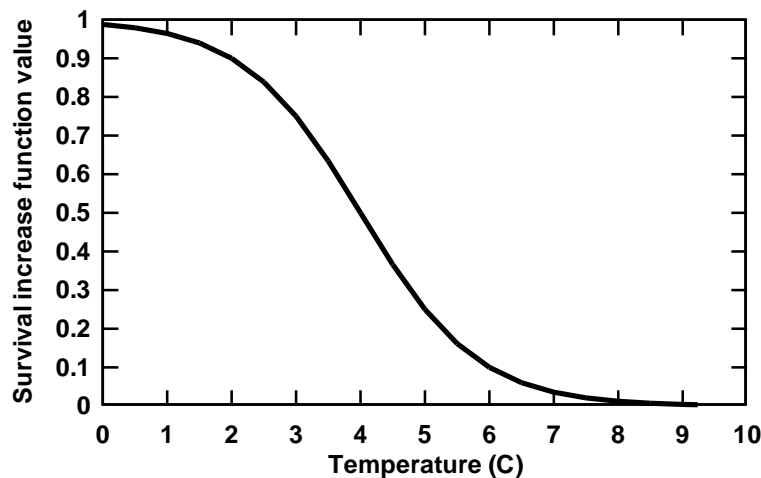
Figure 24. Temperature survival increase function for aquatic predation survival.

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 25). As turbidity continues to increase toward extreme values, aquatic predation risk continues to decrease but is not eliminated.

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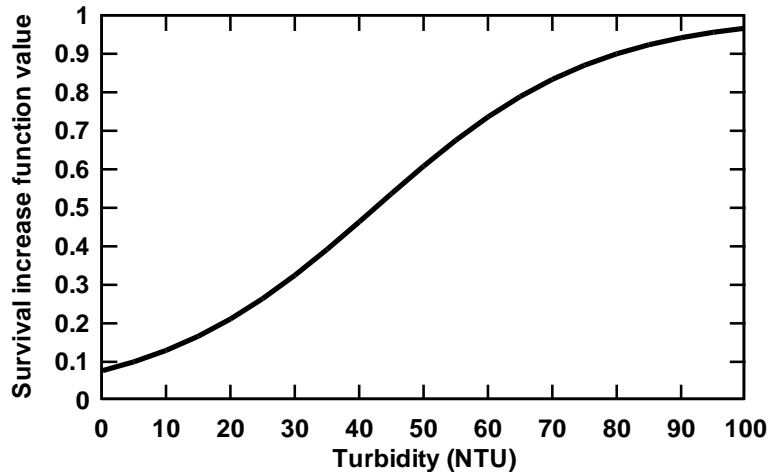
Figure 25. Turbidity survival increase function for aquatic predation survival.

Use of hiding cover. As in the terrestrial predation formulation, use of hiding cover is treated as a survival increase function. The parameter *mortFishAqPredCoverFactor* (unitless) is function value for fish is using the hiding activity and using hiding cover. For fish not using hiding cover, the function value is 0.0.

When hiding, small trout can at least sometimes use small spaces that protect them from larger, predatory trout. A value of 0.95 appears reasonable for *mortFishAqPredCoverFactor*.

Table 17. Parameter values for aquatic predation mortality. Parameter values are for sites where adult trout dominate fish piscivory.

Parameter	Definition	Value
mortFishAqPredDay Min	24-h survival probability due to aquatic predators under most vulnerable conditions, during daytime (unitless)	0.99 (until fit via calibration)
mortFishAqPredNight Min	24-h survival probability due to aquatic predators under most vulnerable conditions, during night (unitless)	0.987 (until fit via calibration)
fishPiscivoryLength	The length at which trout become capable of preying on other trout (cm)	15
mortFishAqPredP9	Predator density at which survival increase function is 90 pct of maximum (cm^{-2})	2×10^{-6}
mortFishAqPredP1	Predator density at which survival increase function is 10 pct of maximum (cm^{-2})	1×10^{-5}
mortFishAqPredD9	Depth at which survival increase function is 90 pct of maximum (cm)	5
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)	8
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)	2
mortFishAqPredT1	Temperature at which survival increase function is 10 pct of maximum (°C)	6
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
mortFishAqPred CoverFactor	Survival increase function value for fish using hiding activity and occupying hiding cover (unitless)	0.95

5.4.5 Terrestrial predation

Predation by terrestrial animals is a dominant source of mortality to trout, 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 trout,

- Are poorer swimmers than adult trout,

- 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 trout are vulnerable, often more vulnerable than small trout;

- Risks are year-round because warm-blooded predators feed as much or more in winter (except those that hibernate or migrate);

- Trout are more at risk when more visible from the air; and

- Risk is higher at night and when trout are feeding instead of hiding.

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 <u>maximum</u> of the independent survival increase functions. This assumption is expressed mathematically as:

terrPredSurv = mortFishTerrPredMin +
[(1−*mortFishTerrPredMin)* × max*(terrPredDepthF, terrPredTurbidityF, terrPredLengthF* ...)].

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.

To represent the difference between day and night in *inSTREAM-SD*, two separate parameters are used for *terrPredSurv*. The parameters *mortFishTerrPredDayMin* and *mortFishTerrPredNightMin* provide separate values for daytime and night. The values of *mortFishTerrPredDayMin* and *mortFishTerrPredNightMin* are each a probability of surviving terrestrial predation for 24 hours under conditions where the survival increase functions are minimal (offering no reduction in risk).

Field data for estimating these minimum survival probabilities are unlikely to be available, so it is best estimated by calibrating the model to observed abundance and habitat use patterns. However, there is some literature from which to estimate a ratio of day to night survival. Recent studies in small streams of coastal California (Harvey and Nakamoto 2013) found 36% of predator attacks on adult trout occurring at night, with birds (including owls, at night) and mammals being the most-common predators. From a review of literature addressing this issue, Metcalfe et al. (1999) reached the general (not site-specific) conclusion that otter and mink are primarily nocturnal but most predation is by birds, which are strictly daytime predators. Metcalfe et al. (1999) estimated that predation risk during foraging by river fish is 150 times greater during daytime than at night, in a system where 90% of mortality was due to birds and fish were active and exposed to predation only 10% of the daytime and 90% of the nighttime. However, at sites where mammals cause a higher percent of the terrestrial predation mortality and where more trout are active in daytime, the difference between night and daytime risks is lower. If we estimate that the mortality risk at night is 70% lower than in the day, a typical value of 0.99 for *mortFishTerrPredDayMin* then produces a value of 0.997 for *mortFishTerrPredNightMin*. (The mortality risk equivalent to survival of 0.99 is 0.01; reducing the risk by 70% results in a mortality risk of 0.003, equivalent to a survival probability of 0.997.) These values are strongly supported by the observations of Harvey and Nakamoto (2013).

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 18). Use of hiding cover is represented in *inSTREAM-SD* as a survival increase function.

First, however, an important note on parameter sensitivity is required. The sensitivity analyses discussed in Section 15.2 of Railsback et al. (2009) show that results of *inSTREAM* can be quite sensitive to the parameters that define how terrestrial predation risk depends on habitat variables. This sensitivity is not surprising, considering that terrestrial predation is normally the only mortality source that adult trout are routinely vulnerable to. Particularly important are the parameters that define the survival increase functions for habitat parameters, especially *mortFishTerrPredD9*, *mortFishTerrPredV9*, *mortFishTerrPredH9*, and *mortFishTerrPredH1*. If these parameters are set in such a way that the survival increase function is very close to 1.0 in several or many cells, then trout occupying those cells can be almost immune to mortality. For example, if the "small stream" parameters for depth illustrated in Figure 26 were used in a large river with many cells having depth greater than 200 cm, then trout in these cells would have very low terrestrial predation risk and could live for many years. Changing the parameter *mortFishTerrPredD9* could greatly change the amount of habitat where predation risk is very low. (In reality, rivers with extensive deep water also likely have predators that can be effective in deep water.) Likewise, if the velocity and distance to hiding cover survival increase functions are very steep and near 1.0 for some cells, some parts of the simulated habitat can be nearly risk-free, producing higher populations of adult trout.

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

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logistic curve: survival increases as depth increases (Figure 26). 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 26 illustrates parameter values for small streams and large rivers (Table 18).
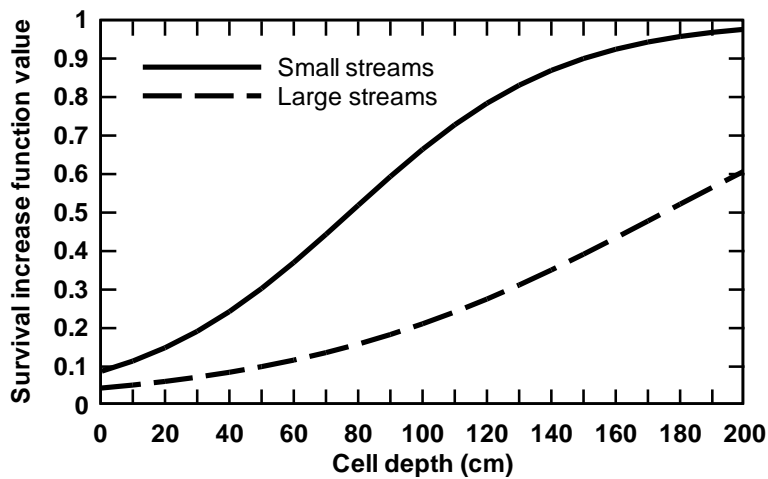
Figure 26. Depth survival increase function for terrestrial predation survival.

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 5.3.3), 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 27).
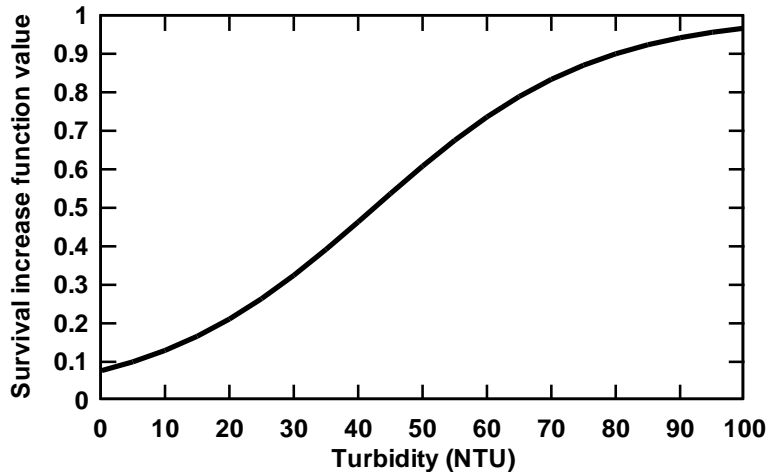
Figure 27. Turbidity survival function for terrestrial predation survival.

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 trout 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 28). These parameter values should be reconsidered for sites where predation is dominated by larger mammals (otters, bears) that strongly prefer large fish.
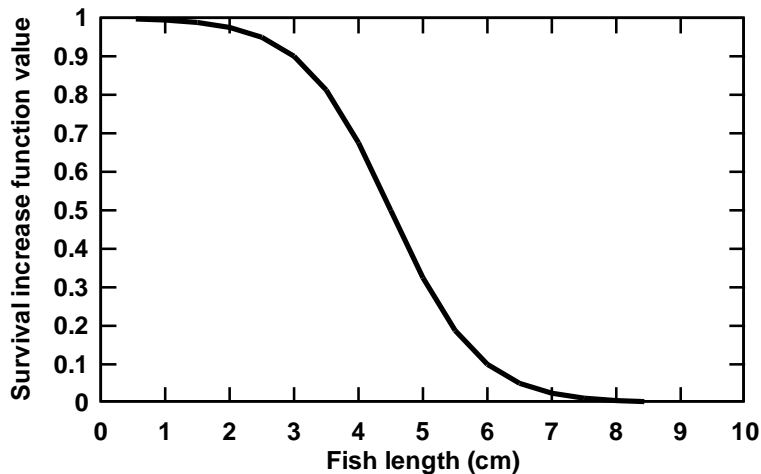
Figure 28. Fish length survival increase function for terrestrial predation survival.

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 trout 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 29). 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 18 and illustrated in Figure 29.
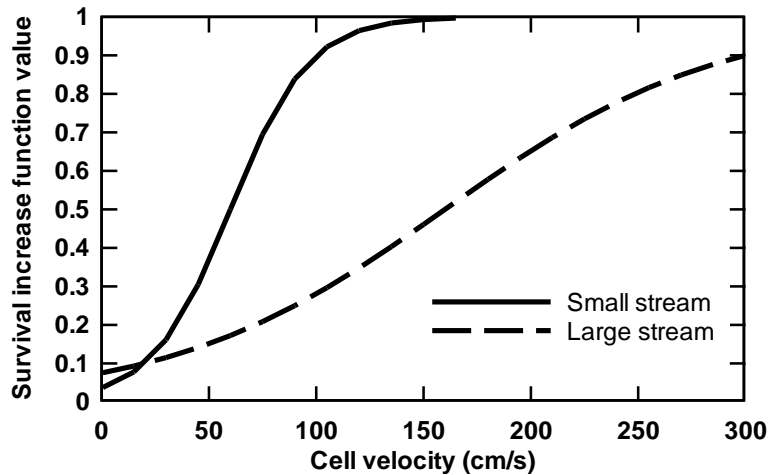
Figure 29. Velocity survival increase function for terrestrial predation survival, with parameters for both small streams and large rivers.

Temperature. No temperature-based survival increase function is included in *inSTREAM* 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 trout at low temperatures can also offset any decreased activity by predators by reducing the ability of trout to escape (Metcalfe et al. 1999). Terrestrial predation can be greatly reduced when rivers freeze over, but ice is not represented in *inSTREAM*.

Distance to hiding cover. Fish that are feeding 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 *inSTREAM*; hiding cover several to tens of meters from a fish can provide at least some predation protection.

Benefits of hiding cover to feeding fish are 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 trout 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 30).
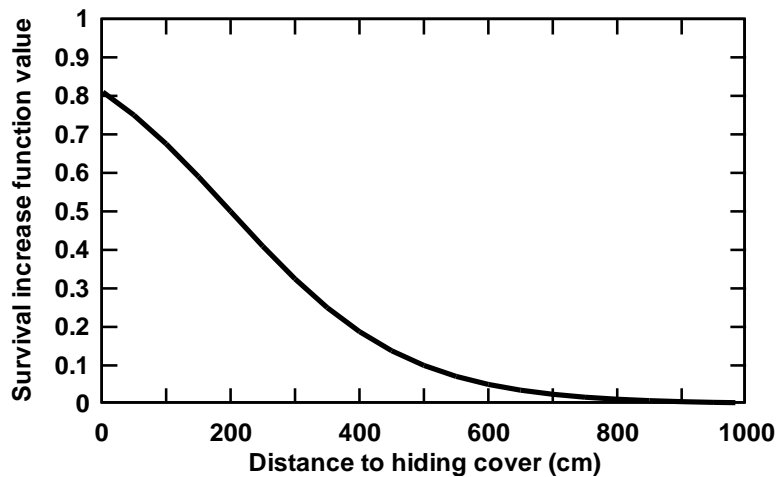
Figure 30. Distance to hiding cover function for terrestrial predation survival.

Use of hiding cover. Fish using the hiding activity instead of feeding can use hiding cover (Section 5.2). In the terrestrial predation formulation, use of hiding cover is treated as a survival increase function, with effects independent of other factors that reduce predation risk. The trout parameter *mortFishTerrPredCoverFactor* (unitless) determines the amount that the survival probability for terrestrial predation is increased if the fish is using hiding cover. If a fish is using hiding cover, then the value of the hiding cover survival increase function is equal to *mortFishTerrPredCoverFactor*; otherwise, the function value is 0.0.

Use of hiding cover makes trout very difficult to find, even with electrofishing equipment, so cover use is expected to greatly reduce the risk of terrestrial predation. On the other hand, recent field experience in small streams found that otters can prey very effectively on trout even when some kinds of cover are abundant (Harvey et al. 2005). We therefore estimate a reasonable value of *mortFishTerrPredCoverFactor* to be 0.95.

Table 18. Parameter values for terrestrial predation mortality.

Parameter	Definition	Value
mortFishTerrPredDay Min	Probability of surviving terrestrial predators for 24 hours under most vulnerable conditions, during daytime (unitless)	0.99 (until fit via calibration)
mortFishTerrPredNight Min	Probability of surviving terrestrial predators for 24 hours under most vulnerable conditions, at night (unitless)	0.997 (until fit via calibration)
mortFishTerrPredD1	Depth at which survival increase function is 10 pct of maximum (cm)	Small streams: 5 Large rivers: 50
mortFishTerrPredD9	Depth at which survival increase function is 90 pct of maximum (cm)	Small streams: 150 Large rivers: 300
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)	Small streams: 20 Large rivers: 20
mortFishTerrPredV9	Velocity at which survival increase function is 90 pct of maximum (cm/s)	Small streams: 100 Large rivers: 300
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
mortFishTerrPred CoverFactor	Survival increase function value when fish are using hiding cover	0.95

5.4.6 Poor condition

Fish in poor condition (low value of the condition factor *K*, weight in relation to length; Section 5.3.1) 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 *inSTREAM*, 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 31; Table 19). 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 31 indicates, the probability of surviving for extended periods becomes quite low when K falls below 0.8.
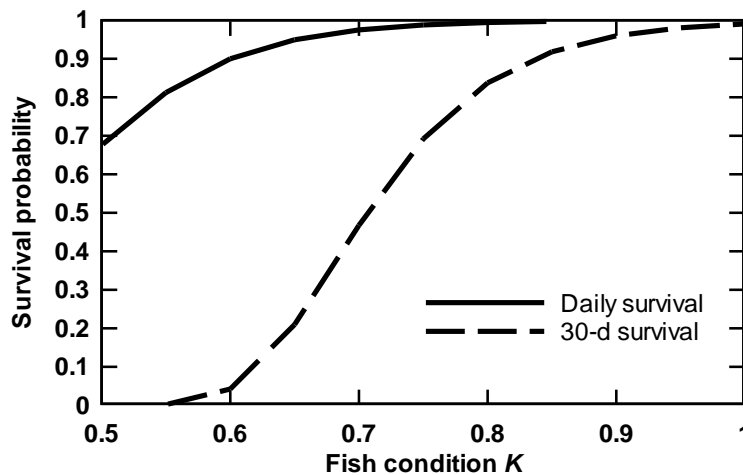

Figure 31. Survival probability function for poor condition. The dotted line is the probability for surviving for 30 d at the value of K.

Table 19. 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 *inSTREAM* should be aware that poor condition mortality can have a strong effect on habitat selection (Section 5.2.2) 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.

5.4.7 Angling and hooking

Angling is a common source of trout mortality in reservoir tailwaters and other sites where *inSTREAM* is likely to be useful, but *inSTREAM-SD* is the only version of *inSTREAM* including it. The angler mortality model includes three separate components: fishing pressure, capture rate, and survival probability. Survival of angling is a function of whether a trout was caught, and the rate at which trout are caught is a function of fishing pressure. Hooking mortality (the subsequent death of fish caught and released by anglers) is modeled as a separate but related mortality source.

The fundamental assumption of the angler mortality formulation is that the risk to an individual fish of being hooked by anglers is a function of fishing pressure and not directly a function of trout abundance. The model assumes anglers catch a constant fraction of the catchable population, so if there are more fish, more are caught. However, the method for predicting fishing pressure includes a term for trout abundance, so abundance has an indirect effect on the risk per trout by changing the fishing pressure. The model also assumes that an individual trout can be caught more than once in a day, which seems not unlikely in heavily-fished sites.

We assume that the trout are not aware of angling mortality risk and how it varies with habitat, and therefore we do not include angling among the risks that trout consider when selecting their habitat. (In fact, this angler mortality formulation does not assume the risk varies among the habitat cells of a reach, although risk can vary between day and night and among reaches.)

Trout that are using hiding behavior instead of feeding (Section 5.2) are assumed immune to angling; their survival probability for angling and hooking is set to 1.0. The following algorithms apply only to fish that are feeding.

Fishing pressure (variable *anglerPressure*) is evaluated as angler hours per day per km of stream, during the daytime. This unit can be compared to commonly measured angler use rates, allowing parameterization and validation of fishing pressure with data on angler use.

Fishing pressure is represented via a set of 12 habitat parameters (*habAnglePressJan–habAnglePressDec*) that provide the value of *anglerPressure* for each month.
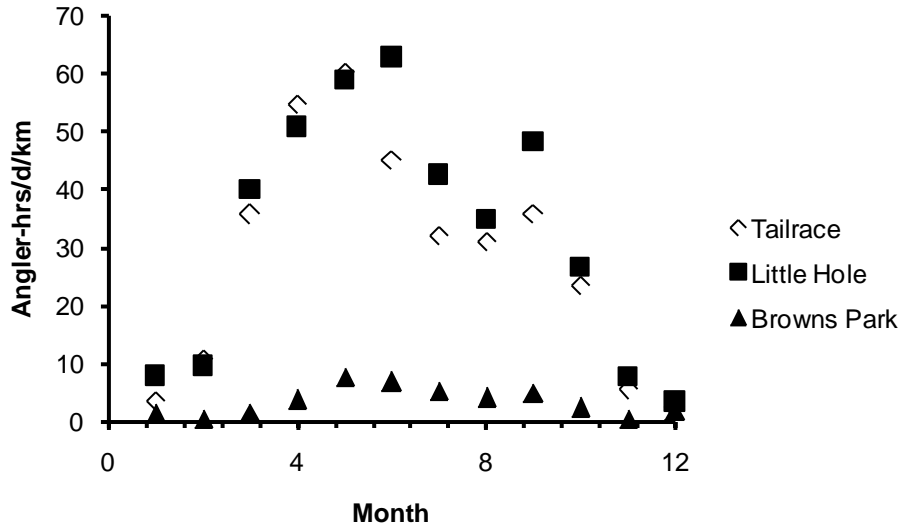
Figure 32. Fishing pressure (boat plus shore) by site and month, from 1992-3 UDWR data.

We also assume fishing pressure is lower at night than during the day. The nighttime reduction in risk is represented by the habitat parameter *habAngleNightFactor* (unitless), which is the fraction by which fishing pressure is reduced at night, year-round. Where night fishing is believed to be minimal, a value of zero should be used for this parameter. Where small numbers of anglers consistently fish at night, for example, *habAngleNightFactor* can be given a value of 0.1 so angling pressure at night is 10% of the daytime value.

Capture rate is represented as the average number of times a fish is hooked per day. This capture rate is assumed to be a linear function of fishing pressure, with the proportionality constant being the parameter *mortFishAngleSuccess*. This parameter represents fishing success as the fraction of catchable fish hooked per angler hour. The value of this parameter can vary among species (e.g., between species that are and are not stocked; Section 8) to reflect differences in vulnerability to angler harvest. Capture rate is also assumed to be a logistic function of trout size. The size dependency reflects the success of anglers in selecting for larger trout by (a) using tackle more attractive to larger fish and (b) fishing in habitat better for large trout.

The capture probability model is:

$$captureRate = mortFishAngleSuccess \times anglePressure \times reachLength \times 10^{-5}$$

$$\times\ logistic(fishLength)$$

where:

- *captureRate* (fish caught per catchable fish per day) has units of d^{-1},
- *mortFishAngleSuccess* (fish caught per catchable fish per angler-hr) has units of (angler-hrs)$^{-1}$,
- *anglePressure* has units of angler-hrs $\times$ km^{-1} $\times$ d^{-1},
- *reachLength* is the length of the modeled reach in cm (input in meters as the parameter "reachLength" in the Reach.Setup file),
- The factor 10^{-5} converts reach length in cm to km, and
- The logistic function of fish length (Figure 33) is defined by two trout parameters *mortFishAngleL1* and *mortFishAngleL9* (Table 20).
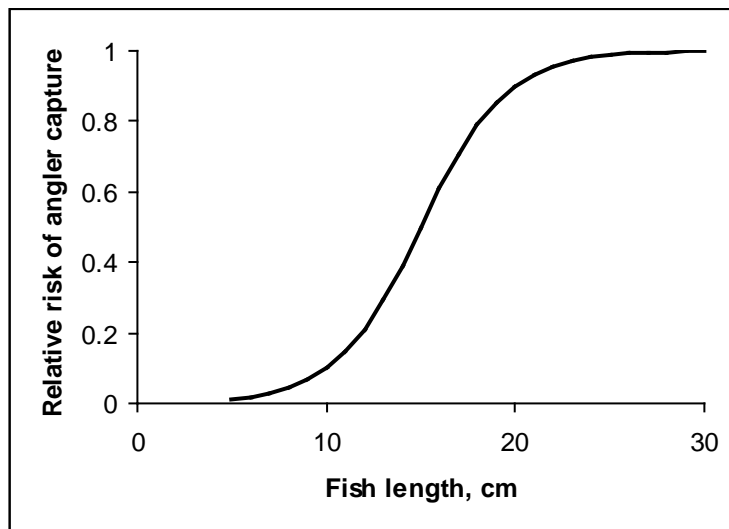
Figure 33. Example fish length function for angler mortality probability of capture.

Multiplying the parameter *mortFishAngleSuccess* by the number of catchable trout feeding in a reach gives the expected number of fish caught per angler-hour, a common measure of angler success. Therefore, this parameter can be estimated and validated if the abundance of catchable trout and angling catch rate are known. Railsback et al. (2006) provide an example estimation of *mortFishAngleSuccess* from abundance and creel census data from the Green River below Flaming Gorge Dam, the source of example parameter values in Table 20.

Note that this capture rate formulation does not include a saturation function for trout density: the probability of any individual trout being hooked does not decrease as the number of trout at a site increases. In reality, when trout are very dense and fishing success high, the fishing effort per angler could be limited by the time required to handle and release hooked fish.

Survival of angling mortality depends on how many times a trout is hooked and whether it is kept vs. released each time hooked.

The number of times a trout is hooked during a time step (variable *timesHooked*) is drawn from a Poisson distribution. A Poisson distribution models the (integer) number of times an event occurs randomly within a specified time period, given an average occurrence rate. Drawing a random value from a Poisson distribution parameterized with the capture rate (average captures per day) and time step size (number of days, in this case a fraction of one day) provides an

integer number of times a fish is hooked during the time step. The value of *timesHooked* is likely to usually be zero or one, but could be two or more.

The primary determinant of whether hooked trout are kept vs. released is assumed to be the local fishing regulations and traditions. However, the fish treated as released also includes fish that shake the lure before the angler has a chance to keep or release them; these fish are assumed to be vulnerable to hooking mortality.

Fishing regulations are represented via parameters that define a "slot limit": it is legal to keep trout that have length less than the value of the parameter *mortFishAngleSlotLower* (cm) or greater than the value of *mortFishAngleSlotUpper* (cm). The values of these parameters can be set to represent a slot limit that protects mid-sized adults, or to represent minimum- or maximum-length limits. (For example, setting *mortFishAngleSlotLower* to 0.0 cm and *mortFishAngleSlotUpper* to 20.0 cm would make it legal only to catch fish > 20 cm long.)

Separate probabilities of keeping hooked fish are applied to fish that are and are not within the legal length ranges. The probability of keeping trout that are of legal length is defined by the parameter *mortFishAngleFracKeptLegal*, and the probability of keeping trout of illegal length is the parameter *mortFishAngleFracKeptIllegal*. The values for these parameters should be selected considering that the fraction kept is the fraction of all fish hooked that are landed and kept, not the fraction of landed fish that are kept: trout that shake the hook before being netted are considered as captured but released.

Each time a trout is hooked, the model first determines whether it is legal to keep, according to the slot limit parameters. Then the appropriate parameter for probability of being kept is identified (*mortFishAngleFracKeptLegal* vs. *mortFishAngleFracKeptIllegal*). A uniform random number is drawn and if the random number is less than the probability parameter the fish is assumed to be kept. Hooked fish that are kept by anglers are considered dead by a mortality source called "angling". Fish that die of angling mortality are not subject to hooking mortality.

Hooking mortality is a risk to fish that are released by anglers. Released trout are assumed to have a constant probability of surviving hooking mortality that is applied each time the trout is hooked. This probability is defined by the parameter *mortFishAngleHookSurvRate*. Trout that do not survive are considered dead by the mortality source called "hooking".

In summary, the following steps are used for each trout to determine the probability of surviving angler harvest. The fishing pressure is updated at the start of each day, being constant within a day and among all habitat cells of a reach.

1. Trout that are hiding are given angling and hooking survival probabilities of 1.0 and excluded from the remaining steps.
2. The daily capture rate is calculated from the fishing pressure and the trout's length.
3. A random draw from a Poisson distribution defined by the capture rate determines the number of times the fish is hooked during the time step (*timesHooked*). If *timesHooked* is zero, the survival probability is 1.0 for angling and hooking mortality.
4. If *timesHooked* is one or more, the slot limit parameters and fish length are used to determine if the trout is of legal length to keep.
5. Steps 6 and 7 are conducted once for each time the trout is hooked.
6. If the trout is of legal size to keep, a random draw is applied to the parameter *mortFishAngleFracKeptLegal* to determine whether the trout is kept. If the trout is not of

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legal size, a random draw and the parameter *mortFishAngleFracKeptIllegal* determine whether the trout is kept. If the trout is kept, the survival probability is 0.0.
7. If the trout is released (not kept), the survival probability for angling is 1.0, but the fish is tagged with the value of *timesHooked*. The trout is then subject to the hooking mortality source.

The survival probability for hooking is evaluated separately, using *timesHooked* as its basis. If *timesHooked* is zero, this survival probability is 1.0. If *timesHooked* is greater than zero (and the fish did not die of angling mortality), the hooking survival probability is equal to the parameter *mortFishAngleHookSurvRate* raised to the power *timesHooked*.

Table 20. Parameters for angler and hooking mortality and example values from Railsback et al. (2006).

Parameter	Definition	Units	Example value
mortFishAngleSuccess	Multiplier to determine capture probability from fishing pressure.	(angler-h)$^{-1}$	0.003
habAngleNightFactor	Factor (0-1) by which fishing pressure is reduced during night.	(none)	0.0
habAnglePressJan	Value of anglePressure for January.	angler-h d^{-1} km^{-1}	3
habAnglePressFeb	(Value of anglePressure for other months.)	angler-h d^{-1} km^{-1}	10
habAnglePressMar		angler-h d^{-1} km^{-1}	35
habAnglePressApr		angler-h d^{-1} km^{-1}	55
habAnglePressMay		angler-h d^{-1} km^{-1}	60
habAnglePressJun		angler-h d^{-1} km^{-1}	45
habAnglePressJul		angler-h d^{-1} km^{-1}	30
habAnglePressAug		angler-h d^{-1} km^{-1}	30
habAnglePressSep		angler-h d^{-1} km^{-1}	35
habAnglePressOct		angler-h d^{-1}	25

		km^{-1}	
habAnglePressNov		angler-h d^{-1} km^{-1}	5
habAnglePressDec		angler-h d^{-1} km^{-1}	2
mortFishAngleL1	Fish length at which relative risk of being hooked is 10% of maximum.	cm	10
mortFishAngleL9	Length at which hooking risk is 90% of maximum.	cm	20
mortFishAngleSlot-Lower	Length defining the lower end of the range in which fish are illegal to keep.	cm	33
mortFishAngleSlot-Upper	The upper end of the range in which fish are illegal to keep.	cm	51
mortFishAngleFrac-KeptLegal	Probability of fish of legal length being kept by anglers.	(none)	0.2
mortFishAngleFrac-KeptIllegal	Probability of fish not of legal length being kept by anglers.	(none)	0.05
mortFishAngleHook-SurvRate	Survival probability for released trout (or trout that shake the hook)	(none)	0.8

5.4.8 Total survival: parameter estimation and effects of fish size, depth, and velocity

The total survival probability for a fish in a particular cell can be calculated by multiplying together the probabilities of surviving separate mortality risks. Figure 34 through Figure 37 illustrate the variation in total survival with fish size, depth, and velocity. They were created by plotting the total daily survival probability for four sizes of trout that all have a condition factor of 1.0, are at a temperature of 15°, feed for 16 h/d, have a minimum survival probability for both terrestrial and aquatic predation (*fishTerrPredMin*, *fishAqPredMin*) of 0.99, and have the values listed above for other parameters. Turbidity and distance to hiding cover were assumed to have no effect on survival, and the density of piscivorous fish was relatively high: one piscivore per five m^2 (density = 2.0×10^{-5}). Fish were assumed not to be using velocity shelters. Predation survival parameters for small streams were used, and angling was neglected. The daily survival is shown on a scale of 0.95 – 1.0 because survival probabilities below 0.95 result in high mortality over several days.

The 3 cm trout (Figure 34) are vulnerable mainly to aquatic predators, as evidenced by the peak in their survival probability at depths of around 10 cm. The 10 (Figure 36) and 20 cm (Figure 37) trout are vulnerable mainly to terrestrial predators and have survival probabilities well above those of smaller trout. The 5 cm trout (Figure 35) are vulnerable to both categories of predators and actually have lower survival than both the smaller and larger trout. Above 5 cm, the range of habitat conditions providing high survival increases with fish size.
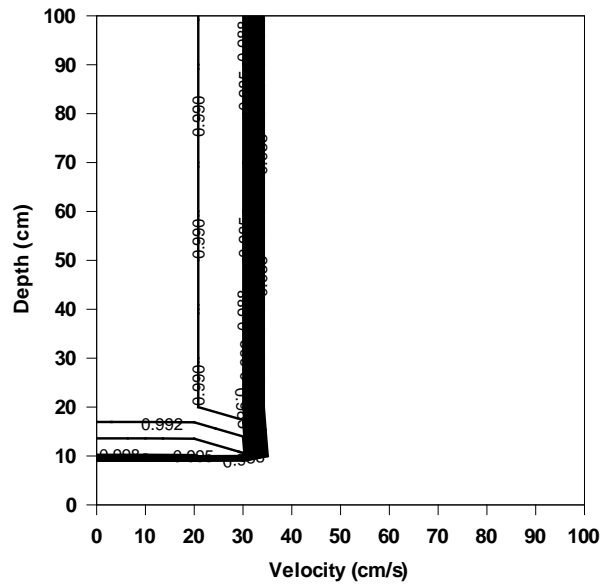
Figure 34. Contour plot of total survival probability as a function of depth and velocity, 3 cm trout.
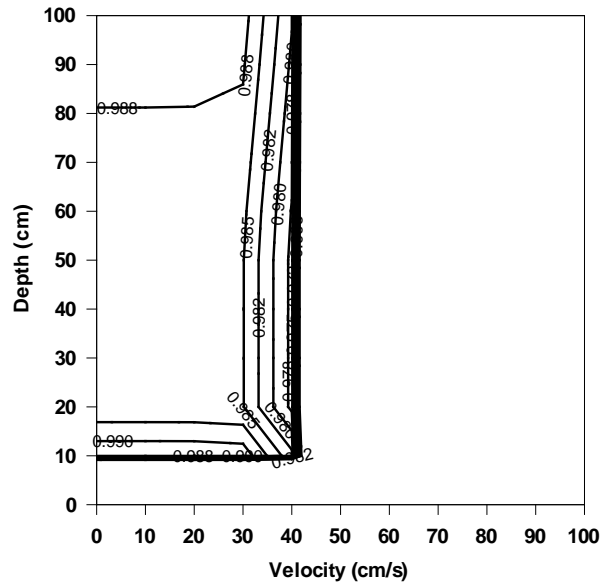
Figure 35. Contour plot of total survival probability as a function of depth and velocity, 5 cm trout.
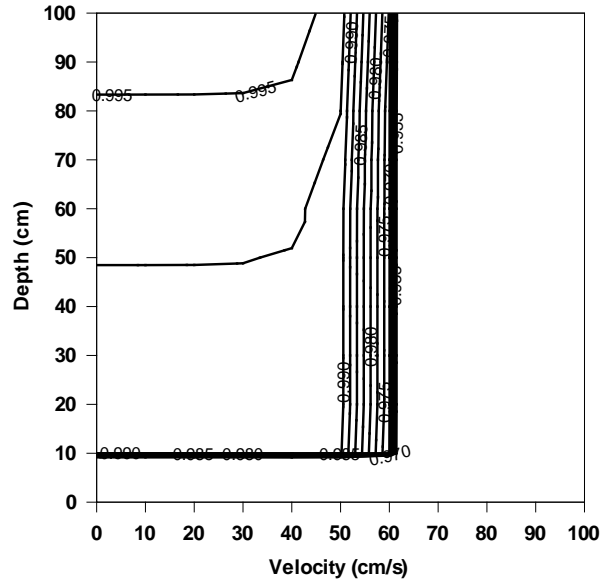
Figure 36. Contour plot of total survival probability as a function of depth and velocity, 10 cm trout.
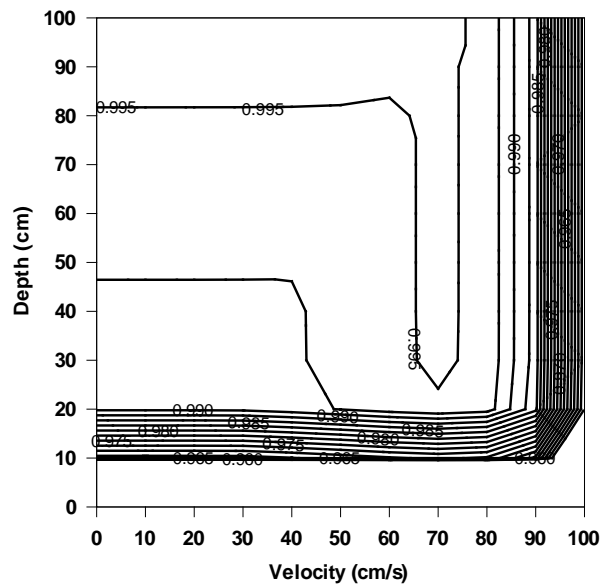
Figure 37. Contour plot of total survival probability as a function of depth and velocity, 20 cm trout.

These survival probabilities are not the only processes affecting mortality rates in the modeled trout populations. The number of fish that die is also a function of the feeding and growth formulation and food availability, and of the trout population's density. Food intake affects poor condition mortality and habitat selection; and because survival probabilities vary with habitat, habitat selection has a major effect on a fish's survival. For example, if food is scarce (perhaps because trout abundance is high) model trout will use habitat where more food is available even if predation survival is low; and predation mortality will therefore increase. As a consequence of these complex interactions, mortality parameter values cannot be estimated well except by calibrating the full model as discussed in Section 17 of Railsback et al. (2009).

5.4.9 Demonic intrusion: experimenter-induced mortality

The graphical interface of *inSTREAM*'s software allows the user to select individual trout 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.

6 Redd Variables and Methods

Redds are the nests laid by spawning trout. When they spawn, female trout typically dig one or several holes in streambed gravel, deposit their eggs in the holes, and cover them. The eggs incubate in the redd until they hatch into new trout, which "emerge" by working their way up through the gravel. In *inSTREAM*, 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 trout. The species of a redd and its initial number of eggs are determined by the female spawner that created the redd (Section 0).

Because of its objectives as a management model, *inSTREAM* 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 *inSTREAM*.

- Some eggs may be diseased, unspawned, unfertilized, or washed out of the redd during its construction.

- 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.

Redds are modeled using the following four daily actions. Scheduling of these actions is discussed in Section 2.3.

6.1 Survival

In *inSTREAM*, 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 and produces similar results when the number of live eggs is high, 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 2.3.

The kinds of mortality represented, and the survival function methods, were selected considering that the objectives of *inSTREAM* focus on flow and temperature effects on trout 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 *inSTREAM* is not designed address to represent gravel quality issues. [The spawning site selection criteria (Section 5.1.2) 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 throughout the reach) 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 *inSTREAM* in situations where these mortality sources are believed to be important.

6.1.1 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 *inSTREAM* 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.

In *inSTREAM-SD*, dewatering survival is calculated from the depth at the daily mean flow, not the hourly flows. Dewatering mortality is a relatively slow process (redds typically retain enough moisture so short dewaterings may have little effect), so use of daily flow is appropriate.

6.1.2 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 trout from emerging. Deposition is especially likely to reduce survival if it includes fine sediment. This redd

mortality source can be very important to trout populations and communities. For example, Strange et al. (1992) found the relative abundance of brown v. rainbow trout in a Sierra Nevada stream to depend on the frequency of winter redd scouring events.

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, *inSTREAM* 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). *inSTREAM* should be considered substantially more uncertain for sites where populations are strongly limited by redd scouring, especially if spawning is limited to pocket gravels (but all models of trout populations or habitat are likely less useful at such sites).

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, *inSTREAM* 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 <u>less</u> <u>than</u> 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 floating-point 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 *inSTREAM* 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 16.6.2 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 trout. Values of 5-10 cm are reasonable for small trout using relatively small gravel; field observations at the Little Jones Creek site found eggs buried as little as 5 cm.

Example scour survival parameters for the Little Jones Creek study site (*habShearParamA* = 0.019, *habShearParamB* = 0.383, *mortReddScourDepth* = 5, 10 cm) produce the decreasing relation between peak flow and survival of redd scouring illustrated in Figure 38.
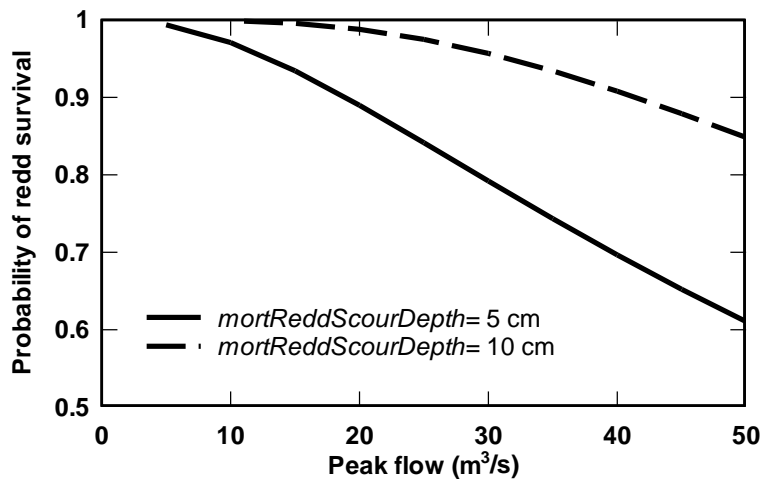
Figure 38. Example redd scour and fill survival function. The Y axis is the probability of the redd not being destroyed during a peak flow event.

This model of scouring estimates the probability of a redd surviving scour <u>in each high-flow event</u>, not on a daily time step. The single survival probability is applied to all redds, assuming that if a redd is scoured then none of its eggs survive. The following steps are used for each redd, on each day. (This algorithm is slightly different in *inSTREAM-SD*, compared to other versions of *inSTREAM*, in using daily peak instead of mean flows.)

- Determine whether the current day's peak hourly flow (the highest hourly flow in the day) in the redd's reach is greater than both the previous day's and the following day's peak 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 hourly peak 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.

As Figure 38 illustrates, redd survival of scouring and deposition is quite sensitive to the value of *mortReddScourDepth*. At the Little Jones Creek sites, for example, using a realistic value of 5 cm produced sufficient scouring to cause the simulated population to often go extinct (the extinction rate is undoubted exaggerated by the lack in *inSTREAM* of immigration of juvenile trout from upstream).

6.1.3 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 trout 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 spring-spawning rainbow trout and fall-spawning brown trout (Table 21; Figure 39) have been determined from data compiled by Brown (1974); Railsback and Harvey (2001) also used the rainbow trout parameters for cutthroat trout. The data compiled by Brown (1974) indicate that rainbow trout spawn at temperatures as low as 3 - 5°C and eggs have a 90 percent survival rate over a 100-d incubation period at 3°C (daily egg survival = 0.999). A daily survival rate of 0.9 (very low long-term survival) was assumed for 0°C, and logistics parameters that reproduce these two points determined. Similarly, Brown (1974) cited data indicating that brown trout egg incubation can take over 150 days at very low temperatures. Parameter values for brown trout were estimated by assuming 90 percent egg survival over 150 days at 1°C (daily survival of 0.9993) and daily survival of 0.9 at 0°.

Table 21. Parameter values for low temperature redd mortality.

Parameter	Definition	Species	Value
mortReddLoTT1	Temperature at which low temperature survival is 10 pct (°C)	Rainbow	-3
		Brown	-0.8
mortReddLoTT9	Temperature at which low temperature survival is 90 pct (°C)	Rainbow	0
		Brown	0
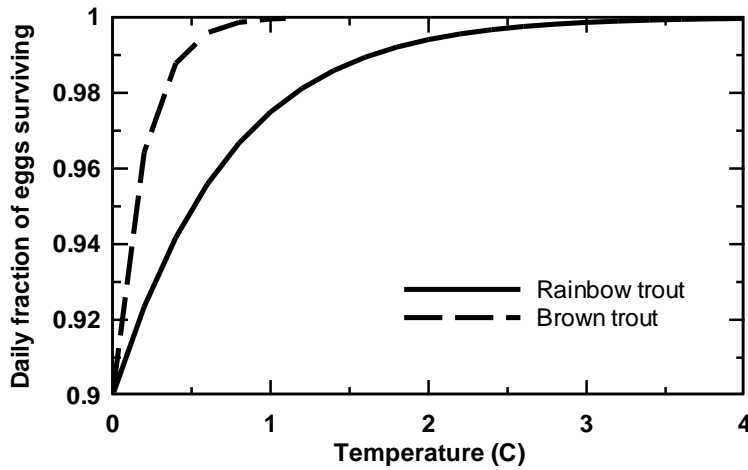
Figure 39. Low temperature redd survival function, for rainbow and brown trout parameter values.

6.1.4 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 40). Parameter values for rainbow trout (also used for cutthroat trout by Railsback and Harvey 2002) are based on interim results of lab studies conducted by the University of California at Davis (Myrick 1998). These data showed daily survival rates declining from about 0.9998 at 11°C to about 0.985 at 19°. The resulting parameter values (Table 22) appear to indicate high survival at high temperatures, but in fact cause low survival if temperatures are elevated for long periods. Parameter values for brown trout in Table 22 were arbitrarily set to 5° less than the rainbow trout values and should not be considered reliable.

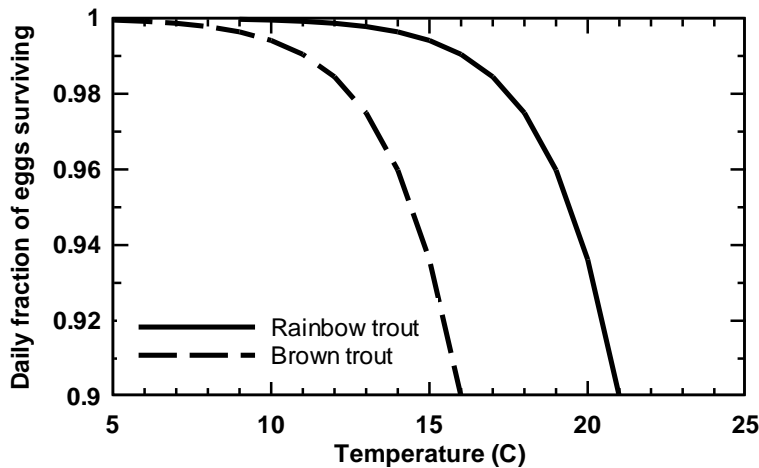Figure 40. High temperature redd survival function, for rainbow and brown trout parameter values.

Table 22. Parameter values for high temperature redd mortality.

Parameter	Definition	Species	Value
mortReddHiTT1	Temperature at which high temperature survival is 10 pct (°C)	Rainbow	30
		Brown	25
mortReddHiTT9	Temperature at which high temperature survival is 90 pct (°C)	Rainbow	21
		Brown	16

6.1.5 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). For simplicity, *inSTREAM* currently 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 used for each redd, for each day:

1. Determining if one or more new redds were created in the same cell on the current day. If not, then superimposition survival is 1.0.

2. If one or more redds (of any species) were created in the same cell, the probability of each new redd causing superimposition (*reddSuperImpRisk*, unitless) is equal to the area of a redd (*reddSize*, cm^2, a fish parameter that can be species-specific) divided by the area of spawning gravel in the redd.

$$reddSuperImpRisk = \frac{reddSize}{(cellArea \times cellFracSpawn)}$$

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

4. 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.

5. Steps 2-4 are executed once for each new redd placed in the cell on the current day.

Note that the value of *reddSuperImpRisk* can be greater than 1.0 if *cellFracSpawn* is very small; in that case, superimposition egg mortality always occurs. In the event that *cellFracSpawn* is zero, there is no risk of superimposition. This assumption is made because there is no gravel to be disturbed by another spawner.

Because of how the parameter *reddSize* is used in this formulation, it is defined as the area a spawner disturbs in creating a new redd. Field observations at the Little Jones Creek site suggest a *reddSize* value of 1200 cm^2 (the area of a circle with a diameter of 35 cm) for relatively small trout.

6.2 Development

To predict the timing of emergence, the developmental status of a redd's eggs is updated daily. The fractional development approach of Van Winkle et al. (1996) is used; this approach is based on accumulated degree-days, a common technique for modeling incubation. These temperature-based methods are simple and reasonably accurate. (Alternative models of salmonid egg development are reviewed by Beer 1999.)

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 this equation:

$$reddDailyDevel = reddDevelParamA + \left(reddDevelParamB \times temperature\right) + \left(reddDevelParamC \times temperature^2\right)$$

The parameters for this equation should be considered likely to vary among species, and among populations that spawn at different times of year. Hatchery management data or literature can sometimes be used to develop or test parameter values. Parameter values for spring-spawning rainbow trout and fall-spawning brown trout were developed by Van Winkle et al. (1996) (Table 23). Railsback and Harvey (2001) found the rainbow trout parameters in Table 23 reasonable for a cutthroat trout population in coastal California.

Table 23. Parameter values for egg development rates.

Parameter	Definition	Rainbow, cutthroat trout value (spring spawning)	Brown trout value (fall spawning)
reddDevelParamA	Constant in daily redd development equation (unitless)	-0.000253	0.00313
reddDevelParamB	Temperature coefficient in daily redd development equation ($°C^{-1}$)	0.00134	0.0000307
reddDevelParamC	Temperature squared coefficient in daily redd development equation	0.0000321	0.0000934

($°C^{-2}$)	

6.3 Emergence

"Emergence" is the conversion of each surviving egg into a new trout 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.

6.3.1 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, *inSTREAM* assumes that 10% of the redd's eggs emerge on the first day of emergence; 20% of the redd's <u>remaining</u> 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 10th 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.

6.3.2 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 random normal distribution with mean equal to the fish parameter *reddNewLengthMean* (cm) and standard deviation equal to the parameter *reddNewLengthStdDev* (cm). However, no fish are given lengths less than half the mean: if the randomly drawn length is less than half the value of *reddNewLengthMean*, a new length is drawn.

- Weight (*fishWeight*, g) is calculated from length, using the length-weight relationship and parameters used in modeling growth (Section 5.3.1) and to create initial fish (Section 7.2). 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

5.2.1). 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 trout is often intense (this intense competition occurs in *inSTREAM*; Railsback et al. 2002).

Example length parameters for newly emerged fish are provided in Table 24. The parameters are from a study of coastal cutthroat trout in Washington (June 1981). This study measured lengths of newly emerged fry found in a downstream trap. A few of these fry had lengths between 2.4 and 2.7 cm, but most were between 2.7 and 3.0 cm. Elliott (1994) observed a coefficient of variation of 0.07 in length at emergence for brown trout at several sites. This value is converted to the standard deviation in length (with a coefficient of variation of 0.07 and a mean length of 2.8 cm, *reddNewLengthStdDev* is 0.2 cm). Parameter values for other species are likely to be available from the literature or from hatchery data.

The previous model of Van Winkle et al. (1996) assumed that bigger spawning females produce bigger eggs, and that bigger eggs produce bigger fish at emergence. This effect of spawner size on offspring size may be important for salmon and large trout where variation in spawner size is large. It is also a mechanism making the offspring of larger fish more likely to be successful. However, relationships among sizes of spawners, eggs, and emergent fish are inconsistent and not well known for most populations. This mechanism does not appear important for the objectives of *inSTREAM*.

Table 24. Parameter values for size of newly emerged fish.

Parameter	Definition	Cutthroat trout value
reddNewLengthMean	Constant for new fish length equation (cm)	2.8
reddNewLengthStdDev	Standard deviation in length of newly emerged fish (cm)	0.2

6.4 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.

7   Initialization

This section describes the methods used to initialize the habitat and fish populations when each new model run is started. Although this section mentions some of the input types and files, complete documentation of file and input types is provided in the separate software guide.

7.1 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 4.1.3). 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.

7.2 Fish Initialization

The initial fish population is built from input data giving the initial abundance, mean length, and standard deviation in length for each age class of each species. (Age classes are defined in Section 3.2.5.) Separate fish initialization data are provided for each habitat reach; each reach's population is built separately.

The methods used to initialize fish are the same as those used to create new fish from redds (Section 6.3.2). The length of each fish is drawn randomly from a normal distribution with the mean and standard deviation specified by fish parameters *reddNewLengthMean* and *reddNewLengthStdDev*. The lengths of initial fish are restricted to being greater than half the mean length for their age class. Weights are calculated from its length using parameters *fishWeightParamA* and *fishWeightParamB*.

Each fish's location is assigned stochastically while avoiding extremely risky habitat. Initial fish are distributed randomly, after which the first day's habitat selection action lets the fish move to more suitable habitat. This approach is designed to be simple and avoid bias in initial locations. However, the method also limits the random distribution of fish to cells where the fish are not immediately at high risk of mortality due to high velocity or stranding. Small fish especially may have a maximum movement distance (Section 5.2.2) too small to allow them to find reasonably safe habitat during their first day's habitat selection, if they are initially placed in a large area of very risky habitat. The following steps are used to assign a fish to its initial cell. These steps are conducted after the habitat reach has been initialized with the flow for the first simulation day.

1. A cell is selected randomly from those in the fish's reach.

2. If the cell has a depth of zero, then step 1 is repeated to identify a new cell.

3. If the cell's velocity puts the fish at extreme risk of high velocity mortality, then steps 1-3 are repeated to identify a new cell. Whether this risk is extreme is determined by (i) calculating the fish's maximum swimming speed in the cell, (ii) calculating the ratio of maximum swim speed to cell velocity, and (iii) determining whether this ratio is greater than the parameter *mortFishVelocityV9*. If so, then the fish's daily probability of surviving high velocity mortality is less than 90%, so steps 1-2 are repeated to select a new cell. Otherwise, the cell becomes the fish's initial location.

4. If steps 1-3 result in Step 1 being repeated 10,000 times without an acceptable cell being found, then the high velocity criterion (Step 3) is abandoned. Steps 5-7 are then followed.

5. A cell in the habitat reach is randomly selected, as in Step 1.

6. If the cell has a depth of zero, then step 5 is repeated to identify a new cell. Otherwise, the cell is accepted as the fish's initial location.

7. If steps 5-6 result in Step 5 being repeated 10,000 times, then model execution is terminated. If this limit is reached, it is very unlikely that there are any cells with non-zero depth.

Fish have a variable *spawnedThisSeason* indicating whether they have spawned during the current spawning season (Section 5.1.1). This variable is set to NO when fish are initialized.

7.3 Redd Initialization

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

8 Trout Stocking

Large numbers of hatchery trout are often stocked in the tailwaters of large reservoirs, a kind of site where *inSTREAM-SD* is especially likely to be applied (because tailwaters also often experience rapidly varying flows for hydropower generation). Stocking can be a critically important source of recruitment for rainbow and cutthroat trout. Therefore, *inSTREAM-SD* simulates stocking.

The stocking method simply adds trout of a user-determined species to the model on selected dates. Hatchery trout are assumed use the same behaviors and parameters as other trout of their species. Because *inSTREAM* allows users to provide separate parameter values for each species (and, via small changes in the model's software, changes in behavior among species), stocked fish can modeled in two ways.

First, stocked trout can be given the same species as other fish being simulated, and they will be identical in characteristics and behavior to other fish of their species. This option may be appropriate if all fish being modeled are of hatchery origin or if differences between hatchery and wild fish are neglected.

Alternatively, hatchery fish can be simulated as a separate species from wild fish, even if both are biologically the same species. Then, parameters (or alternative behaviors, coded separately) for the hatchery fish can be used to implement such assumptions as being unaware of predation in selecting habitat or being familiar only with search, not drift, feeding. However, *inSTREAM-SD* does not include a built-in way to simulate changes in behavior over time that could be used to represent learning or adaptation to river habitat by hatchery fish.

When created, stocked trout are randomly distributed throughout the modeled reach, except that no fish are placed in cells with depth less than 50 cm. To determine its initial location, each stocked fish randomly selects a cell out of all those in its reach with depth > 50 cm. (The model randomly draws a cell and checks whether its depth is > 50 cm. This draw is repeated up to 10,000 times. If no cell with 50 > 50 is found in these 10,000 tries, the model stops.) Stocking is assumed to occur at 10:00 a.m. on the user-specified date. Stocked fish are assumed to feed instead of hide, and to not move among cells, between the time they are stocked and the next model step. Starting with the first model step at or after 10:00 on the day of stocking, stocked trout follow the same schedule and and actions of other trout.

Stocking occurs in the model schedule before movement, so newly stocked trout are given the opportunity to select better habitat before growth and mortality simulations are conducted.

The information needed to define stocking practices is provided by the user as input. The stocking data input file includes one record for each stocking event. Stocking of multiple species or sizes of trout on the same date can be represented with separate records in the input file. The input for each event is:

- Date of stocking (day, month, year),
- Species stocked,
- Reach into which the fish are stocked,

- Number of trout stocked,
- Age of stocked trout,
- Mean length of stocked trout, and
- Standard deviation of trout length.

The length of each individual fish is drawn randomly from a normal distribution with the specified mean and standard deviation. Any lengths that are less than half the specified mean are discarded and a new length drawn. The weight of each fish is assigned from the length-weight relationship for healthy fish (Section 7.2).

9 Random Year Shuffler

One concern in using models like *inSTREAM* is understanding the extent to which results are affected by the choice of years that are simulated. Does a simulation experiment using input from 1990 - 1999 produce the same conclusions as an experiment using input from 1980 - 1989? Would different conclusions be drawn if the input included more wet years and fewer dry years, or if the wet and dry years occurred in a different order? This is one of the potential concerns about model sensitivity that are addressed in Section 15.4 of Railsback et al. (2009), but addressed here because *inSTREAM* has a built-in tool for examining the sensitivity of results to the sequence of input years.

The optional year shuffler in *inSTREAM* can randomize the sequence in which years are simulated. If the year shuffler is turned on, input data are divided into years that start on the month and day that simulations start on. At the start of each such simulation year, a new year is drawn randomly and the model then simulates that year.

Years can be shuffled either with or without "replacement". Shuffling without replacement means that each year of input is used only once, but the order of the years is randomized. Shuffling with replacement means that the years that are simulated are drawn randomly from the range of data and years can be used more than once or not at all. For example, if *inSTREAM* is set up to run from 1990 through 1999 and year shuffling without replacement is used, the sequence of years actually simulated could be: 1994, 1998, 1990, 1997, 1991, 1995, 1993, 1999, 1992, 1996. With replacement, the sequence of years could be: 1998, 1997, 1991, 1997, 1993, 1994, 1993, 1990, 1995, 1990.

The year shuffler works like a time machine, causing the model's clock to jump to a random year at the start of each simulation year. The model's clock then determines which input is used and provides the date that output is labeled with. The following steps are used.

1. The simulation period (defined by the simulation start and end dates specified by the user) is divided into simulation years. A new simulation year starts on each day having the same month and day of the month as the simulation start date. A list of these simulation years is created.

2. The list of simulation years is then randomized, either with or without replacement as specified by the user.

3. Each time the model reaches the beginning of a new simulation year (the month and day of the month are equal to those of the simulate start date), the next year is taken from the randomized list.

4. When the next year is taken from the randomized list of years, the model's clock jumps to that year. The model's clock determines which input data are used, and is used to label output.

For example, a model run is set up to run from 10/1/1990 to 12/31/1995, using year shuffling with replacement. Therefore, there are five simulation years, that start on 10/1 of 1990, 1991, 1992, 1993, and 1995. When the list of years is shuffled with replacement, it becomes: 1991, 1994, 1995, 1992, 1994. Therefore, the model starts with the simulation clock set to 10/1/1991. When the end of the simulation year is completed (simulations for 9/30/1992 are completed), the model's clock jumps to the next randomized year, 10/1/1994. When 9/30/1995 is reached, the clock jumps next to 10/1/1995. When simulations then reach 9/30/1996 the clock jumps to 10/1/1992. At the next 9/30/1993, the clock jumps again to 10/1/1994. Finally, the simulation stops at 12/31/1994.

This example illustrates how using year shuffling can require more input data than non-randomized runs, for model runs set up for a non-integer number of years. In the example, the model run included the period 10/1/1995 through 9/30/1996, even though the model end date was set to 12/31/1995. When the year shuffler is used, input data must be provided for all of each simulation year.

The methods used to determine whether a fish spawns (Section 5.1.1) and whether redd scour mortality occurs (Section 6.1.2) depend on the relation between the current day's flow and the next day's flow. If the year shuffler is used, the value of next day's flow used in these methods is always the actual next day, ignoring year shuffling if the current day is the last day of a simulation year.

10 Random Number Generation

Several processes in *inSTREAM* (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 *inSTREAM* are generated by the MT19937 "Mersenne Twister" algorithm, the default generator in the Swarm software platform used to implement *inSTREAM*. (See SDG 2000 for additional information and references.)

One random number generator is used for all stochastic processes in *inSTREAM*, with one exception described in the following paragraph. 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*. (The software for *inSTREAM* can create replicate simulations automatically; see the Experiment Manager section of the software guide.)

The only stochastic process that uses a separate random number generator is the optional year shuffler (Section 8). The year randomizer uses its own generator and seed (model parameter *shuffleYearSeed*) so that year randomization can be controlled separately. For example, multiple model runs that use the same value of *shuffleYearSeed* but different values of

randGenSeed will produce replicate simulations that all use the same sequence of simulation years.

11 Observation and Output

Individual-based models such as *inSTREAM* are like real ecosystems in that our perception and understanding of them is affected by how we observe them. When *inSTREAM* executes it creates a complex digital world of changing habitat and variable individuals, and the conclusions drawn from simulations can depend very much on what data are collected and reported from the digital world. As with a real ecosystem, it is infeasible to observe everything that happens in *inSTREAM*, so the methods used to observe and report results must be carefully designed.

There are six major categories of output produced by *inSTREAM*, summarized here. The software guide documents how these outputs are controlled and interpreted.

11.1   Graphical Displays

People are best able to absorb and interpret complex information when it is presented visually. Therefore, *inSTREAM* provides a graphical display of habitat cells and the location of fish and redds as the model executes. The size and species of each fish are also indicated. This display resembles looking down on a modeled reach from above.

The graphical display is most useful for understanding patterns of fish habitat use. It is the only output that provides the explicit location of individual fish. While the graphical display produces no numerical output that can be analyzed, it is essential for developing understanding and belief in the model, especially its habitat and habitat selection methods.

11.2   Summary Population Statistics

It would be very cumbersome and unhelpful to output the state of each individual fish over time, so instead summary statistics are generated from *inSTREAM* and reported via file output. These statistics include abundance, mean and maximum fish length, and mean and maximum fish weight; all broken out by species, age class, and habitat reach. The software is easily modified to obtain additional output variables or to break statistics out by additional factors.

11.3   Habitat and Habitat Use

The kind of habitat that is available, and what habitat types are used by fish, is often of management or research interest. Therefore, *inSTREAM-SD* includes an optional output file that reports output on habitat availability and use: the area, habitat variable values, and number of fish in each habitat cell. These outputs can be used, for example, to identify depths and velocities that are preferred or avoided by simulated fish.

11.4   Fish Mortality

Understanding how many fish die of each mortality source is often important. When model trout die, the cause of their death is recorded. Output describes the cumulative number of fish that have died of each mortality source.

11.5   Redd Status and Mortality

Redd output reports when a redd was created, how many eggs were created, and when the redd was removed from the model because all its eggs had died or emerged. Redd mortality output reports how many eggs, from each redd, died from each redd mortality source.

11.6   Intermediate Output

The previous five kinds of observations can be considered "final" results: they describe what happened during simulations, but not why individuals behaved as they did. Intermediate results include the state and decisions of individuals as they proceed through each day's actions. Output of intermediate results can be important for testing and understanding the model. For example, if a particular kind of fish (e.g., small juvenile trout) exhibits an unexpected behavior— using deep instead of shallow habitat—intermediate output will be needed to understand whether this unexpected behavior is due to a flaw in the habitat selection method or is simply the result of an unusual situation (e.g., a lack of hiding cover in shallow cells).

inSTREAM provides two facilities for intermediate output. One is "probes" opened from the graphical display. These are windows that can be opened to manually observe and control the variables of individual fish, redds, and habitat cells. The second facility is a variety of optional output files that provide intermediate results for testing the model and its software.

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