Individual-Based Model Formulation for CutthroatTrout, Little Jones Creek, California

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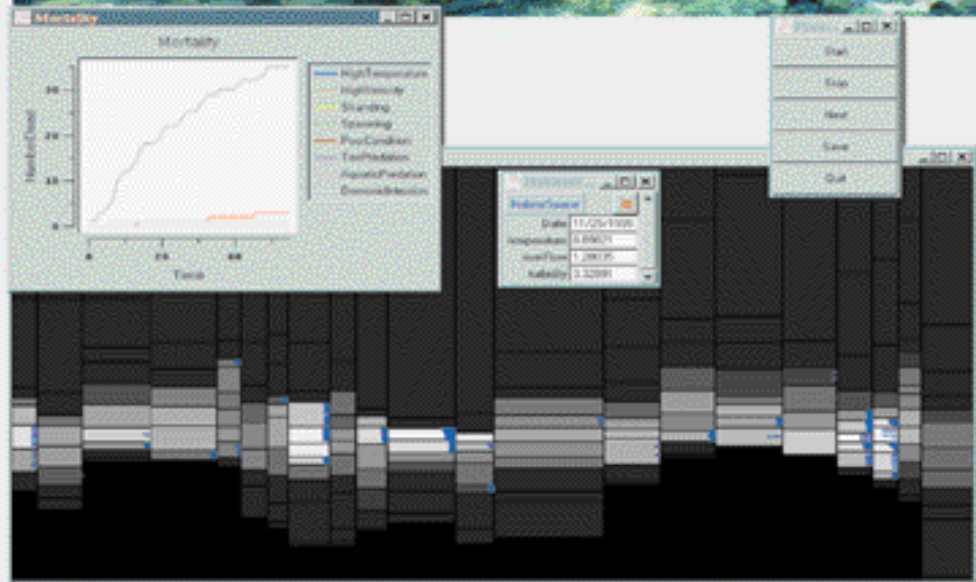
Pacific Southwest Research Station

Forest Service
U.S. Department of Agriculture

Abstract

Railsback, Steven F.; Harvey, Bret C. 2001. **Individual-based model formulation for cutthroat trout, Little Jones Creek, California.** Gen. Tech. Rep. PSW-GTR-182. Albany, CA: Pacific Southwest Research Station, Forest Service, U. S. Department of Agriculture; 80 p.

   This report contains the detailed formulation of an individual-based model (IBM) of cutthroat trout developed for three study sites on Little Jones Creek, Del Norte County, in northwestern California. The model was designed to support research on relations between habitat and fish population dynamics, the importance of small tributaries to trout populations, and the usefulness of individual-based models for forest management. The model simulates the full trout life cycle at a daily time step; habitat is modeled at a resolution of several square meters. The major trout activities simulated are spawning, habitat selection (movement), feeding and growth, and mortality. Two feeding strategies are simulated: drift feeding and searching for stationary food. Mortality risks include starvation, aquatic predation, terrestrial predation, high temperature, stranding, and high velocity. Movement maximizes the probability of surviving and attaining reproductive size over a future time horizon. Risks to incubating trout eggs include extreme temperatures, dewatering, and scouring by high flows. The model design approach was adapted from complex adaptive systems theory.

Retrieval Terms: cutthroat trout, habitat selection, individual-based model, population model, salmonids

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In Brief . . .

This report documents the formulation of an individual-based model (IBM) of the cutthroat trout population of Little Jones Creek, Smith River drainage, Del Norte County, in northwestern California. The model is being built as a research joint venture of the USDA Forest Service's Pacific Southwest Research Station, Redwood Sciences Laboratory, and Lang, Railsback, & Associates, using the California Individual-based Fish Simulation System (CIFSS). The CIFSS is a modeling approach and software package for IBMs of stream fish. The main objective of the Little Jones Creek cutthroat trout model is to evaluate the IBM approach for management applications, such as predicting the individual and cumulative effects of timber harvest, water diversion, and habitat alteration on fish populations. The model will also be used to test hypotheses about the mechanisms of habitat selection by stream salmonids over daily and seasonal time scales and evaluate the importance of small tributaries to stream trout populations.

The model uses a number of key features and assumptions, including a 1-day time step for all model processes and a spatial resolution of several square meters. Habitat is modeled as rectangular cells with dimensions typically in the range of one to several meters across the stream and several meters in the longitudinal direction. Stream flow, water temperature, and food availability are the variables driving the model over time; food is the primary limiting resource for trout; and trout have complete knowledge of the mortality risks and food availability in a specific area of surrounding habitat. The model simulates three kinds of objects: habitat cells, fish, and redds (nests created by spawning trout).

We adapted a theoretical approach to IBM from the emerging science of complex adaptive systems. Two key principles of this approach are that IBMs are more powerful if realistic behavior patterns emerge from simple, fitness-maximizing rules for individual behavior; and the modeled behavior of individual fish is more realistic if the fish base their decisions on outcomes predicted over some time horizon instead of on the immediate outcome.

Habitat cells determine their depth and velocity from the daily stream flow rate; this calculation uses a lookup table imported from an external hydraulic model. The popular Physical Habitat Simulation (PHABSIM) and River Habitat Simulation (RHABSIM) hydraulic models can be used to create the lookup tables. Habitat cells also track the availability of food, velocity shelters for drift-feeding fish, hiding cover, and spawning gravel.

The fish in our model conduct four major actions each day:
- Spawning: Adult fish spawn if they meet a number of readiness criteria. Upon spawning, fish find appropriate habitat and create a new redd, with the number and size of eggs depending on the spawner's characteristics.

- Movement: Each fish examines the surrounding area each day and moves to the site with the best accessible habitat. Defining the "best" habitat is crucial and has been a major focus of our research. We assume fish move to habitat offering the highest probability of surviving and growing to sexual maturity over a specified time

horizon (e.g., 90 days). Survival and growth to maturity are functions of habitat-related mortality (e.g., extreme temperatures), predation mortality, and food intake, which affect starvation mortality, and growth.

- Feeding and growth: We simulate energy intake resulting from both stationary drift feeding and active searching for benthic food and overhead drop-in. Intake varies with depth, velocity, turbidity, fish size, food availability, and food depletion by competing fish. Energy costs of swimming also depend on the feeding strategy and the availability of velocity shelters. We assume fish use the more profitable of the two strategies, and calculate growth from energy intake and consumption using standard bioenergetics methods.

- Survival: Daily survival is a function of high temperature, high velocity, stranding by inadequate depth, spawning stress, starvation, and predation. Our predation formulation includes separate functions for terrestrial and aquatic predators, with survival probabilities that vary with depth, velocity, hiding cover, temperature, turbidity, and fish size.

Redds are modeled from when they are created until all eggs have died or emerged as new fish, with the development rate a function of temperature. Redds can suffer egg mortality due to dewatering at low flows, scouring at high flows, high or low temperatures, and superimposition of new redds.

I. Introduction

Because of concern about fish stocks at risk of extinction, such as stocks of Pacific salmon, many large-scale resource management efforts have been implemented, including the Northwest Forest Plan (NWFP). One significant weakness of existing information to support management efforts is the inability to link habitat conditions to the dynamics of populations. This situation is partly attributable to the historical tendency to view habitat requirements and population dynamics as separate research topics. Most previous research on the habitat requirements of Pacific salmonids has not been process-oriented and has not attempted to link the availability of habitat features to changes in population size. Conversely, existing population models for salmonids are too general to predict the effects of specific habitat changes on populations. One consequence of this failure to link habitat directly to population dynamics is that little or no guidance is available to managers attempting to prioritize activities for the conservation of threatened and endangered fishes.

The recent development of individual-based models (IBM) for fish populations (Van Winkle and others 1993) could be a major step forward in guiding management decisions. In particular, spatially-explicit versions of these models directly predict the consequences for fish populations of changes in physical habitat and biological conditions. However, these models are at an early stage of development. Readily testable, useable models are urgently needed.

Although the ultimate goal is to provide useful tools to managers, the Little Jones Creek cutthroat trout model serves as a prototype to allow testing of the IBM approach. In addition to evaluating the IBM approach for management applications, such as predicting the individual and cumulative effects of timber harvest, water diversion, and habitat alteration, the Little Jones Creek cutthroat trout model will be used to address hypotheses about the mechanisms of habitat selection by stream salmonids over daily and seasonal time scales, and to evaluate the importance of small tributaries to stream trout populations. Evaluating the effectiveness of the approach for a particular population will determine if it should be applied more broadly.

The primary objective of this report is to fully document the methods and parameters that were implemented in the software of the IBM for Little Jones Creek cutthroat trout. The predictions of IBMs are potentially dependent on all of the detailed assumptions, equations, parameter values, and schedules used in the model, and on how these are implemented in computer code. This document describes how the model is initialized by defining the habitat and starting fish populations, then describes the methods used to simulate habitat, fish, and redds. The model schedule, which has an important effect on simulation results, is specified explicitly. The report also identifies topics for future model development and research.

The report is organized to allow readers to develop a general understanding of the model before encountering all its details. Sections II through VI provide information on the major components of the model, but ignore some details for clarity. Section VII describes methods for calibrating the full model and calibration completed to date. Section VIII presents a description of field data collection methods appropriate for this model and how they differ from conventional instream flow modeling approaches. Section IX contains full descriptions of the more complicated details of the model. Priorities we have identified for future research related to this model are documented in Section X. The cutthroat trout model is built with the California Individual-based Fish Simulation System (CIFSS), a system for designing and coding individual-based fish models. The computer software that implements this formulation (including parameter and input file formats) is described in a separate user guide (Railsback and others 1999b). This formulation document uses the same input parameter names as the computer code and compiles them into a master list of model parameters (Section XI).

I.A. Fundamental Approach and Assumptions

This model is built around a theoretical approach to individual-based modeling that we have adapted from the emerging science of complex adaptive systems. A key principle of this approach is that IBMs are more powerful if realistic behavior patterns emerge from simple, fitness-maximizing rules for individual behavior. Most IBMs depend heavily on rules that impose specific behaviors on the model animals; these rules are often designed to force behaviors that have been observed in the field to be reproduced in the model. We prefer to avoid such "imposed behavior" rules, and instead try to give our model fish the freedom to make whatever choices maximize simple objectives that are clearly and directly related to their fitness.

A second key principle we follow is that the modeled behavior of individual fish is more realistic if fish make decisions by maximizing a variable more closely related to evolutionary fitness, rather than focusing on factors such as instantaneous growth and survival rates. Other IBMs and much of the optimal foraging literature attempt to explain animal behavior by using only the immediate outcome of a decision (e.g., selecting habitat to maximize instantaneous food intake or survival probability). Instead, we assume animals base decisions on the consequences over some time horizon, which can lead to significantly different results. For example, maximizing instantaneous survival probability for most fish would result in merely hiding from predators, while maximizing survival over the next 90 days requires a fish to eat enough to avoid starvation risks. Because the ability to base decisions on predicted future outcomes provides a significant fitness benefit, it seems unreasonable to model behavior without considering how animals predict the consequences of decisions to their fitness over times much greater than 1 day. This principal has been explored and supported by Bull and others (1996), Mangel (1996), Railsback and others (1999c), Railsback and Harvey (2001), and Thorpe and others (1998).

This IBM formulation is for resident coastal cutthroat trout. We use the following fundamental assumptions:

- All model processes, such as stream flow and temperature, fish movement, foraging, growth, mortality, and spawning occur on 1-day time steps.

- The spatial resolution is several square meters. Habitat is modeled as rectangular cells with dimensions typically in the range of one to several meters across the stream and several meters in the longitudinal direction. Cell borders are chosen to minimize the habitat variation within cells while capturing the stream's natural variation among cells.

- The external variables driving the model over time are stream flow, water temperature, turbidity, and food availability.

- Flow, temperature, and turbidity are constant over space. We assume that food availability parameters (the mass of drift food per volume of stream water and mass of stationary food per stream area) are constant over both space and time. (Simulating realistic spatial variation in food availability, and its effect on fish, is a long-term goal of our modeling program; Section X.B.4.)

- Fish compete for food, not habitat space. We assume that the food intake of a fish is a function of the total food available in a habitat cell (a function of cell size, depth, and velocity) and the amount of food consumed by more dominant fish in the cell. This allows fish densities to vary realistically with food availability and the need to avoid mortality risks.

- The fish activities driving trout habitat selection are spawning and feeding. Only habitat characteristics related to these activities are simulated. We do not, for example, simulate use of habitat for hiding and resting when not feeding; we assume all fish can find such habitat.

- Trout move in response to spatial variation in food intake and survival probability. We assume fish are "intelligent" enough to correctly predict their food intake and survival probabilities in different habitat cells and determine which cell offers the highest fitness (Section IV.B.2). We do not assume or simulate any learning by fish. (Note that, although we assume fish correctly perceive the actual food intake and survival probabilities at potential destinations, alternative assumptions are possible; e.g., Section X.C.2.)

I.B. Study Site

Little Jones Creek is a third-order tributary of the Middle Fork Smith River, in Del Norte County, northwestern California (*fig. 1*). Resident cutthroat trout are the only fish present; a barrier at the mouth of the creek prevents upstream migration of anadromous fish. Harvey (1998) provides a more complete description of the watershed.

The trout model is being applied to three separate reaches of Little Jones Creek; these are approximately 1,000 m upstream of the mouth, 3,300 m upstream of the mouth, and a first-order tributary entering the creek at about 3,300 m upstream.
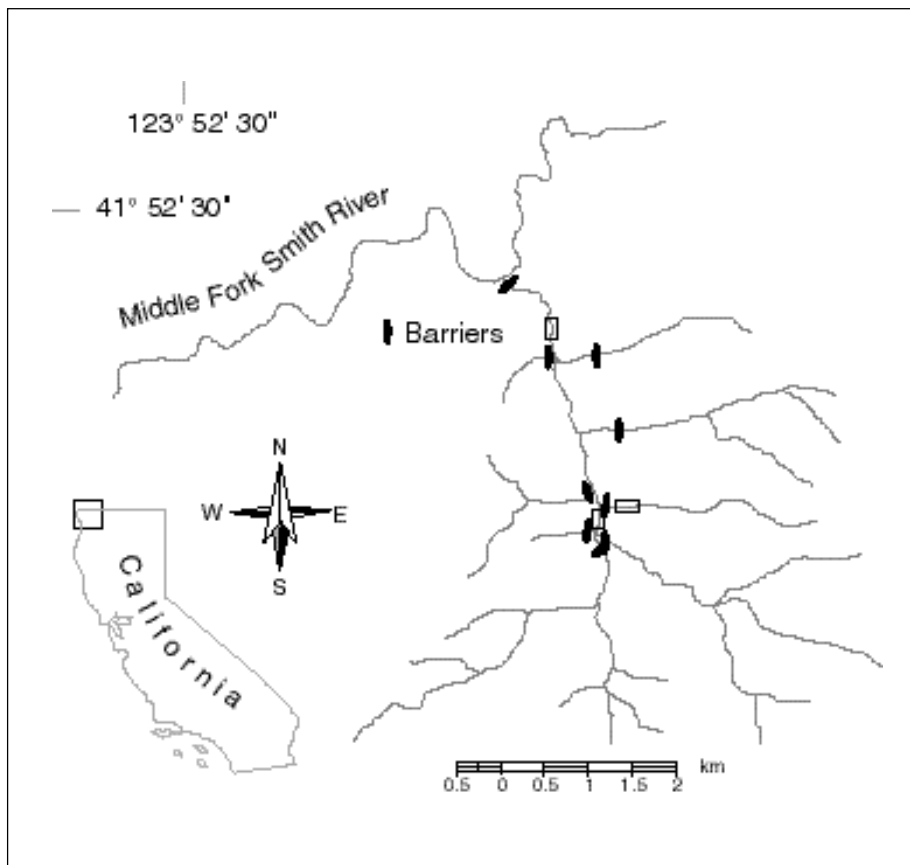
Figure 1 —Study site at the Little Jones Creek of the Middle Fork Smith River in Del Norte County, northwestern California. Modeled reaches are enclosed in rectangles.

I.C. Conventions

I.C.1. Units

This formulation and the CIFSS software use length units of centimeters (cm), weight units of grams (g), and temperature in Centigrade (°C). Stream flow is in units of cubic meters per second (m^3/s).

Because the model uses a daily time step, most time-based parameters use day as the time unit. However, there are several exceptions to this convention; for example, flow and velocity variables are per second. Most food intake calculations use hourly rates because the number of hours per day that fish feed is variable.

Fish lengths are evaluated as fork lengths throughout this model formulation. All weight variables for fish and prey (food) use wet weight.

I.C.2. Parameter and Variable Names

So that the parameter names in this report match those in the model code's input files, we follow the naming conventions used in the *Swarm* simulation software used to code the model (Railsback and others 1999b). 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"; see the list of parameter names in Section XI).

We use the convention of starting input parameter names 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 by the model.

I.C.3 Survival Probabilities and Mortality Sources

A number of factors can cause fish or fish eggs to die in our model. We refer to these factors as "mortality sources." (The term "mortality rate" typically is used to mean the daily probability of dying, equal to one minus the survival probability.) Although we use the word "mortality" in parameter names and our text, the model formulation bases all mortality-related calculations on survival probabilities. This convention simplifies computations and reduces the chances of error: the cumulative survival of several mortality sources is calculated simply by multiplying the individual survival probabilities together.

I.C.4. Dates, Days, and Fish Ages

This model uses input in the "MM/DD/YYYY" format (e.g.: 12/07/1999) for dates. The software converts this input to an internal date format that automatically accounts for leap years.

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.

We follow the convention that fish are age 0 when born, and the age of all fish is incremented on January 1.

I.C.5. Habitat Cell Conventions

We developed our own conventions for describing the rectangular cells used to model habitat. These conventions were designed to correspond with computer graphics conventions (so that habitat is mapped correctly by our software) and to correspond with terms used in popular instream flow models.

"Transects" and "Cells"—Habitat is modeled as rectangular, two-dimensional, depth-averaged "cells"; depth and velocity are modeled for each cell and assumed uniform within the cell. Cells fall along a "transect," a straight row of cells across the stream and floodplain perpendicular to the direction of flow. (The word "transect" also commonly refers to a line across the channel

along which depth and velocity is measured. Because we do not necessarily use this data collection approach, we use "transect" to refer to a row of cells.) The number of habitat cells usable by fish varies with flow: cells on the stream margins may be dry at low flows.

X and Y Dimensions—Because the hydraulic model we use is one-dimensional, our model assumes the river is straight with all velocities in one direction. The X and Y values referred to here are coordinates (in cm) of cell boundaries.

The X dimension is defined to be in the downstream-upstream direction. Because the origin (X = 0) is at the downstream end of a reach, water flows from right to left on an X-Y plot. The Y dimension is across the channel. To correspond with computer graphics, which place the origin (X,Y = 0,0) at the top left of the screen, we define Y to be zero on the left bank facing upstream.

Distances between Cells—Some calculations in the model require values for the distance between two cells (e.g., for finding the cells that are within a fish's maximum movement distance). Because cells are two-dimensional, there is no single distance between two cells; as a convention, we evaluate the distance between two cells as the straight-line distance between the centers of the cell.

II. Model 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 only in the separate user guide (Railsback and others 1999b).

II.A. Habitat Initialization

A model run starts by reading in the habitat characteristics that do not change during the simulation. These characteristics are the location and dimensions of habitat cells, the values of habitat cell variables that do not change with time (the fractions of cell area with velocity shelters and spawning gravel, distance to hiding cover), and the lookup tables used to calculate daily depth and velocity in each cell. (Habitat cells and these variables are described in Section III.)

II.B. Fish Initialization

We build the initial fish population from input data giving the number, mean length, and variance in length for each age of each species. The input file for initial fish populations can provide data for multiple dates (e.g., all dates on which the population at the study site was censused so that the model can be started at any of these dates). For the Little Jones Creek study site, model simulations typically start around October to take advantage of the most accurate population estimates. (Fish population estimates are most accurate in the fall because low late-summer flows provide good counting conditions and young-of-year fish are relatively large and observable.)

Lengths (cm) for each fish are drawn from a lognormal distribution, the mean and variance of which is provided as input. To avoid unrealistic values (e.g., negative lengths) when a high variance is specified, the lengths of initial fish are restricted to being greater than half the mean length for their age class. The weight (g) of each fish is calculated from its fork length using a length-weight relation whose parameters are input. (This relation is also used to calculate growth in length from a change in weight; see Section IV.C.)

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

Table 1 — *Parameter values for length-weight relation.*

Parameter	Definition	Units	Value
fishWeightParamA	Length-weight relation multiplier	[1]g/cm^3	0.0124
fishWeightParamB	Length-weight relation exponent	none	2.98

[1]Approximately; this is an empirical parameter in which units vary with fishWeightParamB.

This is not a standard length-weight regression relationship. It is intended to be a site-specific length-weight relation for fish in good condition.

Parameter values for this relation *(table 1)* were calculated from fish observations made at the Little Jones Creek study sites. They were based on observations of fish in relatively good condition, with weight per length that is slightly higher than average. We determined these parameter values using fish collected approximately monthly throughout 1998 and 1999. Standard condition factors (100,000 times weight over length cubed) were calculated for each observed fish. We used log-log regression to estimate the parameters from the length and weight of fish that had standard condition factors between 1.1 and 1.3.

By initializing fish using the length-weight relation used in the growth routine, we build in the assumption that fish are initially in good condition. This assumption reflects observed low variation in condition among individuals and over time for cutthroat trout in Little Jones Creek.

Each fish's location is assigned randomly to one of the habitat cells. The first day's movement simulation puts the fish in reasonable starting locations. However, we do not assign fish to cells where the depth is zero because some small fish may have a maximum movement distance (Section IV.B.2) too small to allow them to find reasonable habitat on the first move.

We initialize fish assuming that no fish have recently spawned at the time they were initialized (Section IX.A.7). This assumption should be reconsidered if the model is initialized during a spawning season.

II.C. Redd Initialization

In this model we have not provided the capability to initialize the model with redds present.

III. Habitat Model

The habitat component of our model simulates hydraulic conditions (depth and velocity), temperature, and food availability (a function of food production and the number of fish competing for it).

We follow the lead of preceding habitat models (Bovee 1982) and IBMs (Van Winkle and others 1998) by representing stream habitat as a collection of rectangular, two-dimensional, depth-averaged cells. However, we have made the important improvement of carefully designing the habitat cell sizes and placement to avoid scaling errors common in other models. In modeling habitat at our Little Jones Creek site, we considered these factors in representing habitat as cells:

- Cell sizes should be appropriate for the scale over which fish use and select habitat. There is little conclusive literature on the most appropriate scale for fish-habitat interactions, but it seems clear that fish select habitat over longer distances than the spatial resolutions typically used in PHABSIM habitat suitability studies.

- The very small or narrow cells typically used in PHABSIM models likely would induce major edge-effect errors in an IBM where we model

competition among multiple fish for the resources available within each cell.

- Cells should be placed to capture the full range of hydraulic variation and complexity of the stream being modeled. Capturing this variation is more important to the model's accuracy than any difficulties that may be encountered in calibrating the hydraulic model to such habitat (Railsback 1999).

- Cells should be placed to minimize habitat variation within each cell, because the model assumes habitat is homogeneous within cells.

The methods we developed for implementing these considerations are provided in Section VII.

III.A. Cell Boundaries and Dimensions

All the cells on one transect have the same length in the X (upstream-downstream) dimension, but vary in width, the Y (across channel) dimension. For each transect, the user provides the X coordinate for the upstream end of the cells. For each cell, the user provides the Y coordinate of the cell's right boundary. These coordinates are measured in the field. This input allows the model to determine the extent of each cell in both dimensions.

III.B. Daily Flow, Temperature, and Turbidity

At the start of each daily time step, the model reads in the day's river flow (m^3/s), temperature (°C), and turbidity (nephelometric turbidity units, NTU). Flow is used only to calculate the depth and velocity in each cell, and for several criteria used to determine when fish spawn (Section IX.A). Turbidity data are used in the model of drift food intake (Section IX.C.2) and predation mortality (Sections IX.D.6 and IX.D.7). (We do not model the potential effects of turbidity on production of fish food.)

We assume these parameters are constant over relatively short reaches that do not contain tributaries, including our sites at Little Jones Creek. We also neglect diurnal variation in them. Diurnal variation in water temperature at Little Jones Creek averaged only 1.1 °C (maximum 2.6 °C) between May 1998 and May 1999.

III.C. Depth and Velocity

The depth and velocity of each habitat cell (and the number of cells that have water) vary with the river discharge. The hydraulic models we currently use neglect changes in channel direction and cross-channel flows, so water velocity has only one component (downstream).

To take advantage of existing stream hydraulic modeling software and avoid having to include hydraulic simulations in our model, we import lookup tables of depth and velocity, as a function of stream flow, for each cell. These depth and velocity lookup tables are generated by external hydraulic simulation software. This approach allows all the hydraulic model building, testing, and calibration to be conducted in specialized hydraulic software, prior to running our model. We used RHABSIM (TRPA 1998) to generate the depth and velocity look-up tables for Little Jones Creek, but any hydraulic model capable of providing data on the scale of habitat cells could be used in conjunction with the fish model.

Daily velocities and depths for each cell are interpolated from the values in the lookup table. Because both depth and velocity are assumed by the hydraulic models to be logarithmically related to flow, we use log interpolation. To make this computationally efficient, we store the base-10 logarithm of the flows, depths, and velocities as they are read in from the lookup table. Then, when depths and

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velocities are needed for a daily flow rate, we use the log of daily flow and linear interpolation to find the corresponding log(velocity) and log(depth) for each cell. For zero depth and velocity values, in the lookup table, we set the log to -1. If the interpolated log value of depth or velocity is less than or equal to -1, then we set the value to zero. (Using values lower than -1 to represent the log of zero values causes unrealistic interpolation results when depths or velocities are very low but non-zero.)

For any flows below the lowest in the lookup table, we extrapolate the depth and velocity downward from the lowest two flows. The need to make this extrapolation can be avoided by making sure the lookup table includes flows lower than any we need to simulate. RHABSIM can model depths and velocities down to zero flow.

Likewise, for flows above the highest in the lookup table, we logarithmically extrapolate depth and velocity upward from the highest two flows. If this produces unrealistic results, the lookup table can be extended to higher flows using the hydraulic model or manually edited to put in extremely high flows.

III.D. Velocity Shelter Availability

We assume that a constant (over time) fraction of each habitat cell has velocity shelters available for use by drift feeding fish (Section IX.C.3); shelters also affect the high velocity mortality risk (Section IX.D.2). The user provides as input the fraction of each cell with velocity shelter (variable "cellFracShelter"). These fractions should include any part of the cell with complex hydraulics that could be used by trout to reduce their swimming energy. 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 could provide such shelters. (We recognize that velocity shelter availability can vary with fish size and flow, but do not model such variation because of its complexity. Addressing this issue is one of our research priorities; Section X.B.3.)

We assume each fish uses up an area of velocity shelter equal only to the square of its length (Section IX.C.3). This assumption is designed to maintain our overall assumption that fish compete for food, not space. A fish has access to shelter if the amount of shelter available in its habitat cell (the cell area times the fraction of the cell with velocity shelter) is greater than the area of the cell already used by more dominant fish. This means that a fish has access to shelter if there is any unused shelter space available for it.

III.E. 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 includes small pockets of gravel behind boulders as well as more classic spawning beds. The user provides these spawning gravel fractions (variable "cellFracSpawn") as input.

III.F. Distance to Hiding Cover

The model includes a habitat input variable that is an estimate of how far a fish in the cell would have to move to find hiding cover. This variable (cellDistToHide, m) is used in the terrestrial predation mortality model (Section IX.D.6).

III.G. 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 poorly understood. Although some studies (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 IBMs. Modeling food production is also complicated by the multiple sources of food available to fish. We assume all food is either "drift" food, moving with the current, or "search" food that is relatively stationary and must be searched out by the fish. Both drift and search food may originate with benthic (stream bottom) production or from terrestrial input.

Our model assumes fish compete for the food available in each habitat cell. Therefore, the habitat model includes methods to determine for each cell: how much food is available each day, and how much is consumed by fish.

III.G.1. Production

In the absence of established models of trout food production, we developed models that are simple yet mechanistic and easily calibrated using observed trout growth and survival (Section IX.C.6). We make the simple assumption that the concentration of food items in the drift ("habDriftConc," grams of prey food per cm^3 of stream water) and the production of stationary food items in the stream benthos or overhead drop-in available via the search feeding strategy ("habSearchProd," grams of prey food produced per cm^2 of stream bottom per hour) are constant over time and space.

(We considered trying to simulate how food is produced in specific habitats like riffles and depleted by fish as it travels downstream, as in the feeding model of Hughes (1992b). However, the model of Hughes (1992b) shows that simulating drift depletion over space would require a major increase in the complexity of our food production and availability model. Our approach appears to capture the general food competition dynamics in a much simpler model.)

Our feeding formulation allocates the amount of drift and search food available per hour in each cell among fish (Section IX.C.5). These hourly rates are determined by the physical characteristics of habitat cells. The total amount of search food available ("searchHourlyCellTotal," g/h) is simply the cell area multiplied by habSearchProd.

The total drift food available in a cell ("driftHourlyCellTotal," g/h) is a function of the cell's cross-sectional area and average water velocity, the drift food concentration parameter habDriftConc, and a drift regeneration parameter "habDriftRegenDist":

$$driftHourlyCellTotal\ (g/h) = 3600\ s/h \times cell\ width\ (cm)\ \times\ depth(cm)$$
$$\times\ velocity\ (cm/s) \times habDriftConc\ (g/cm^3)$$
$$\times\ [cell\ length\ (cm)\ /\ habDriftRegenDist\ (cm)].$$

The last term in this equation 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 transects with cells 2 m long would have five times the food availability of one 10 m-long transect. This term keeps the amount of food available (and the consequent density of fish) from being an artifact of how transects are spaced.

The parameter habDriftRegenDist has units of centimeters and should theoretically have a value approximating the distance over which drift depleted by foraging fish is regenerated. This parameter is actually used to calibrate habitat selection and survival of starvation (Section IX.C.6). Smaller values of

habDriftRegenDist provide higher amounts of food in a cell. The parameter habDriftConc also affects the amount of food in a cell, but unlike habDriftRegenDist, it also affects food capture rates of drift-feeding fish (Section IX.C.2).

Estimation of preliminary values for these food parameters is discussed in Section IX.C.6, and calibration values are provided in Section VII.A.

III.G.2. Availability

When a fish is conducting its daily evaluation of potential movement destinations (Section IV.B), it considers how much food is available to it in each cell. We model food availability to a fish as the total food production, minus the food consumed by any other fish that have moved into the cell. Because fish movement occurs in descending order of fish size, larger fish have access to food before smaller fish do. Availability is tracked separately for drift and search food.

At the start of each day, the total daily food availability is calculated for each cell, for both drift and search food. Total daily availability is equal to the hourly production rates described above (Section III.G.1) times the number of hours per day we assume fish feed (Section IX.C.1).

Each time a new fish moves into a cell, its food consumption is subtracted from the food remaining available for additional fish. When a fish's consumption is limited by the amount of food available in the cell (Section IX.C), its consumption will equal the remaining availability and no food will be available for additional fish. Any fish moving into a cell where all the food is consumed by larger fish will consequently have zero food consumption.

III.H. Day Length

Day length ("dayLength," in hours) is used in the food intake routine and is calculated from the Julian date (day of the year, 1-365) and site latitude (habLatitude, an input parameter). We use equations modified from the Qual2E water quality model (Brown and Barnwell 1987):

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

where:

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

For the Little Jones Creek site, habLatitude is 42 degrees.

Day length is used to estimate the number of hours per day available for fish to feed. Although nocturnal feeding may be common in salmonids, Young and others (1997) observed primarily daytime feeding by Colorado River cutthroat trout during summer.

IV. Fish Model

This section describes the methods used by the model's fish. We use the same methods for all fish (except incubating eggs and embryos) regardless of age or size.

Fish carry out daily four sets of actions: spawn, move to maximize fitness, feed and grow, then survive or die according to survival probabilities that vary with habitat cell and fish characteristics. The order in which these actions are scheduled is discussed in Section VI.B.

The coastal cutthroat trout (*Oncorhynchus clarki clarki*) is closely related to the rainbow trout (*O. mykiss*), and they have similar life history characteristics (Stearley 1992). Because less laboratory and field information is available for

cutthroat than for rainbow trout, in many parts of the formulation we use equations and parameter values originally developed for the latter.

IV.A. Spawning

The objectives of this model require simulation of the full life cycle and I.A). Our long-term research goals include making the spawning methods more compatible with our mechanistic, fitness-based approach by letting fish select their spawning date on the basis of their energetic condition, predicted habitat conditions, and the consequent predicted spawning success (Section X.A.2).

We make two major simplifying assumptions in the spawning formulation. First, we only track spawning actions for females. We also neglect the energetics of spawning: the energy costs of gonad production, weight loss upon spawning, etc., except for a spawning mortality function.

IV.A.1. Determine Spawn Readiness

Fish in the model can spawn only on days when a number of fish- and habitat-based criteria are met. These spawning criteria (described in Section IX.A) limit spawners to fish in good physiological condition and restrict spawning to times when physical conditions (dates, flows, temperatures) are likely to be successful. The criteria for readiness to spawn do not include a requirement that good spawning habitat be available; this formulation is guided by the assumption that trout will spawn whether or not "classic" spawning habitat is present.

On the days when all the spawning criteria are met for a fish, then it has a random probability of spawning equal to the variable "fishSpawnProb." This stochastic selection of spawning date gives the model user some control over what percent of spawning-sized fish actually spawn; if the value of fishSpawnProb is low compared to the number of days in the spawning period (e.g., 1/fishSpawnProb is greater than the number of potential spawning days), then some potential spawners will probably not spawn. It also imposes variation in the date fish spawn; without this probabilistic approach, an unrealistically large number of fish would spawn on the first day when spawning day criteria are met.

Before calibration, we estimate the value of fishSpawnProb to be 0.016, the inverse of the number of days in the spawning period. This value was estimated from limited spawning observations in Little Jones Creek, which indicated that spawning occurs approximately from April 1 to June 1, a period of 62 days.

IV.A.2. Identify Redd Location

The model incorporates the observation that trout select specific ranges of depth, velocity, and substrate without attempting to simulate the mechanisms by which these variables affect redd success. We adopt a PHABSIM-like approach of weighting potential sites by their habitat suitability, then having the spawner select the best available cell of those within moving distance. Superimposition (Section IX.E.5) is likely to result from this formulation because fish actively search a large area for the best spawning habitat. However, the best cell for spawning can vary from day to day as flow varies.

The spawner selects the cell that (a) is within moving distance and (b) has the highest value of variable "spawnQuality" where:

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

The variables spawnDepthSuit and spawnVelocitySuit are habitat suitability factors determined using methods described in Section IX.B. The value of

spawnGravelArea is the cell area times its fraction with spawning gravel. The spawnGravelArea is included in spawnQuality because we assume a fish, even if it does not select for bigger patches of gravel, is more likely to spawn in a cell that has more area of gravel.

We assume that spawners can move the same distance for spawning as they can each day to improve their food intake and survival probabilities (Section IV.B.2). This formulation does not allow long spawning migrations, which are not feasible anyway in the limited study reaches we model. (Spawning habitat appears ample in Little Jones Creek.) We assume that fish move to the cell that they select for spawning, even though they are likely to move from it during the same day's movement process. When they have identified the cell in which to spawn, we set the fish's location to this cell.

Spawning movement overrides feeding habitat selection. To spawn, fish move into cells regardless of other fish in the cell. Multiple females can also spawn at the same site on the same day.

IV.A.3. Make Redd

Each spawner creates a redd. The number of eggs in the redd (the spawning female's fecundity) depends on the spawner's characteristics, according to this equation.

$$numberOfEggs = fishFecundParamA \times fishLength^{fishFecundParamB}$$

We use the parameter values that Van Winkle and others (1996) obtained for brown trout from Avery (1985). These parameter values *(table 2)* result in fecundities of 60 eggs for a spawner of our minimum spawning size of 12 cm (Section IX.A.6), and 220 eggs for a spawner of 20 cm, corresponding well with a small number of observations of fecundity at and near the Little Jones study site and the findings of Carlander (1969).

IV.B. Movement

Fish movement is a very important process to simulate realistically because movement is probably the most important mechanism available to stream fish for adapting to short- and mid-term changes in habitat and fish state. Daily fish movement results in patterns of predicted habitat selection that are easily tested against observed patterns. For the model to meet its objectives, it must produce realistic habitat selection patterns.

Modeling movement has been a primary focus of our research in developing this model. We reviewed methods used in previous models and developed our own approach, documented by Railsback and others (1999c). We developed the following principles for modeling movement:

- The model will be most general and powerful if realistic movement emerges when we give fish simple decision rules for responding to the environment and realistic information about the environmental complexities to which they must respond. Restrictions that force the model to reproduce a specific observed behavior that is not ubiquitous (for example, territoriality) should be avoided.

Table 2—*Parameter values for fecundity.*

Parameter	Definition	Units[1]	Value
fishFecundParamA	Fecundity (eggs per redd) multiplier	[1] 1/cm³	0.11
fishFecundParamB	Fecundity exponent	none	2.54

[1]Approximately; this is an empirical parameter with variable units.

- Stream fish are generally aware of their surrounding environment and are able to make movement decisions in much less time than our 1-day time step.

- In a model such as ours where both food consumption and mortality risks are spatially variable, realistic movement decisions must consider both food intake and mortality risks.

- The simplest, most believable decision rules maximize some direct measure of an animal's fitness.

- To make realistic decisions, modeled animals must consider outcomes predicted over some upcoming time period. It is unreasonable to assume that an animal makes its decisions considering only the immediate, same-time-step outcome.

Simulating fish movement involves two related steps: a fish determines whether to move each day (using the "departure rules"), and determines the destination it moves to (using the "destination rules"). Our formulation does not explicitly assume fish are territorial. Instead, the density of fish in each cell is an emergent property of how fish move to maximize their individual fitness. Each fish's decision whether to move into a cell is a function of how much food the fish would get there and what its probability of survival would be. Fish move to maximize their fitness, where fitness is defined as the expected probability of surviving over a specified time horizon multiplied by the fraction of reproductive size attained over the time horizon. This formulation was selected following a detailed review of alternatives (Railsback and others 1999c). Our movement approach was successfully tested by demonstrating its ability to reproduce six important patterns of trout habitat selection. Not all of these habitat selection patterns were reproduced by alternative approaches, such as maximizing net energy intake or minimizing immediate mortality risk (Railsback and Harvey 2001).

IV.B.1. Departure Rules

We use a simple departure rule: fish examine potential destinations every day and move to a location offering higher fitness if one is available. This method assumes fish are aware of their surroundings and know when better habitat is available nearby (Hughes 1992a). This method allows fish to escape habitat that becomes poor (cells that go dry when flow decreases; excessive velocities during floods). The model therefore reproduces the observed ability of trout to move in response to events like flood flows (Harvey and others 1999).

IV.B.2. Destination Rules

We assume fish move to the habitat cell that is accessible, as limited by a maximum movement distance and exclusion of cells where depth is zero; and provides the highest value of the fitness measure used to evaluate destination cells. This approach is implemented by using the following steps.

Move in Order of Dominance—The destination rules are dependent on fish moving in order of decreasing dominance, implementing the assumption (tested by Hughes 1992a) that stream salmonids rank feeding positions by desirability and the most dominant fish obtain the most desirable sites. The most dominant fish move first and cannot be displaced by smaller fish. Dominance in the model is determined by fish length; Hughes (1992a) showed that dominance is usually, but not always, proportional to length for arctic grayling. The significance of prior residence to territorial defense and movement of salmonids (Cutts and others 1999, Johnsson and others 1999) is not currently included in the model.

(In determining the dominance of each fish, the model multiplies fish length by the parameter sppDomFactor. By using different values for different species, this parameter allows dominance to be a function of species as well as length. In single-species models like this cutthroat model, sppDomFactor has no effect on

results, but the parameter must be included in the parameter input file and it must have a value greater than zero.)

Identify Potential Destination Cells—A distance limitation, barriers, and depth can limit potential destination cells. The number of fish already in a cell does not limit its availability as a destination. Following our approach of having fish compare conditions between its current cell and destination cells, our term "destination cells" does not include the cell a fish is currently in.

Distance limitation. A habitat cell is excluded as a potential destination if it is beyond a certain distance. The maximum movement distance should be considered the distance over which a fish is likely to know its habitat well enough to be aware when desirable destinations are available, over a daily time step. The maximum movement distance is not necessarily a function of the fish's swimming ability.

We assume the maximum movement distance is a function of length. Because we assume mobility and spatial knowledge increase rapidly with fish size, we use an exponential function. The parameters should be considered site-specific. For example, fish may explore larger areas in lower-gradient rivers.

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

Our model lets fish follow a gradient toward better habitat if the gradient is detectable within the maxMoveDistance, but it does not give fish 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.

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 and others 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 for the model. Movement rates (m/d) reported in the literature are also potentially deceptive because they are generally not based on continuous or even daily observations of location.

However, the literature observations do indicate that adult trout commonly move distances up to 300 m. Harvey and others (1999) showed fall and winter movements of adult (18-24 cm length) cutthroat trout of up to about 55 m in 1 day at the Little Jones Creek study site. 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.

We selected parameter values (*table 3)* to 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.

Table 3—*Parameter values for fish movement distance.*

Parameter	Definition	Units[1]	Value
fishMoveDistParamA	Multiplier for maximum movement distance	none	20
fishMoveDistParamB	Exponent for maximum movement distance	none	2

[1] fishLength (fork length) and maxMoveDistance are both in cm.

These move distance parameters could preclude very small fish from having any potential destination cells if cells are large. This artificial barrier to movement (an artifact of the model's spatial scale) could be important, for example, by preventing newly emerged fish from moving from the cell where their natal redd was to habitat where survival probabilities are higher. In such a situation, competition among new fry for food would largely be an artifact of the cell's size, which controls how much food is in it (Section III.G). To address this problem we always include as potential destinations four cells bordering the sides of a fish's current cell.

Movement distances vary among individuals and over time. This variation could be induced in the model by making the value of the parameter maxMoveDistance variable (Section X.C.2).

This formulation provides another advantage to rapidly growing fish: they are able to look further for good habitat.

Barriers. In one of the Little Jones Creek study sites (a small tributary) there are cascades large enough to block upstream movement of trout. These barriers affect the potential destinations available in movement. (We define "barrier" to mean a blockage to upstream, but not downstream, movement.) For cells upstream of a trout's current cell, the effect is straightforward: if there is a barrier between the trout and an upstream cell, then the upstream cell is excluded as a potential destination. We do not simulate the possibility of barriers being passable to large trout but not to small ones; we assume no fish can pass upstream over a barrier.

For cells downstream of a trout's current cell, the effect is less straightforward. We assume fish consider as movement destinations those cells that they are familiar with, as determined by the variable maxMoveDistance. However, it does not seem reasonable to assume a fish would be familiar with the habitat in a cell that is downstream of a barrier; the barrier makes it impossible for the fish to have explored the cell and returned to its current cell. Fish movement downstream over barriers occurs, with the fish apparently making an uninformed assumption about the consequences of moving downstream. Making such "blind" movements seems most likely to be successful if they are undertaken only when the alternative of not moving downstream is very risky. Therefore, we model downstream movement over barriers in this way:

- Cells that are within maxMoveDistance from a fish, but downstream of a barrier, are included as potential movement destinations.

- We assume the fish is not familiar with the habitat at such cells and therefore cannot predict the "expected maturity" fitness measure used to evaluate destinations (Section IV.B.2). Therefore, we assume the fish will cross downstream over a barrier if, and only if, none of the alternative cells (which do not require crossing the barrier) have an expected maturity value greater than 0.5. (This means the fish will not cross a barrier unless its expected survival at alternative sites is very low, but when expected survival at alternatives is low, the fish always crosses the barrier.)

- If a fish does cross downstream over a barrier, we place the fish in a cell just across the barrier and then repeat the whole movement process. This means a fish can cross several barriers in a day, and possibly (if conditions for survival are poor) move all the way down the modeled reach.

Minimum depth. We exclude cells as destinations if they have depth 0. This rule is imposed only to reduce computer execution times. The fitness measure that determines movement gives fish a very strong incentive to avoid moving to dry cells, where the risk of mortality by stranding is very high. However, specifically excluding movement to dry cells significantly reduces the computations needed to select a destination cell, with very little anticipated effect on model results.

We do not, however, require a fish to move if the depth in its current cell drops to zero. But in that situation, the fish must either move or suffer stranding mortality. In addition, if the flow decreases so that the nearest cell with non-zero depth is farther away than a fish's maximum movement distance, then the fish suffers stranding mortality (Section IX.D.3).

Evaluate Potential Destination Cells—A fish evaluates each potential destination cell to determine the fitness it would provide. We use the "expected maturity" fitness measure of Railsback and others (1999c). Each fish has to evaluate its potential fitness in each potential destination cell (and its current cell), because the fitness measure is a function of the fish's size and species and of the cell characteristics.

Individual fish select the potential destination cell providing the highest value of "expectedMaturity" where:

$$expectedMaturity = nonstarvSurvival \times starvSurvival \times fracMature.$$

The variable "nonstarvSurvival" is the calculated probability of survival for all mortality sources except poor condition, over a specified time horizon given by the variable "fishFitnessHorizon." This probability of survival is calculated assuming that the current day's survival probabilities will persist for the number of days specified by "fishFitnessHorizon." The value of "nonstarvSurvival" is calculated as:

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

where S_i, S_{ii}, S_{iii}, etc. are the daily survival probabilities (the unitless probability of surviving for one day) for various mortality sources ($i,ii,…$), evaluated for the current day, fish, and cell (Section IX.D). The value of nonstarvSurvival is determined for the fish's size before the daily growth that would occur at the potential destination cell; this assumption is made to simplify the model's software. (It would be more consistent with the rest of our model to calculate nonstarvSurvival by using the fish size after the growth it would obtain at the destination cell; however, we expect the effect of this assumption to be negligible in almost all cases.)

The value of "starvSurvival" is the probability of surviving the risk of poor condition (closely related to starvation; Section IX.D.5) over the number of days specified by "fishFitnessHorizon." This term introduces the effects of food intake to the fitness measure. The value of starvSurvival is determined by these steps (Railsback and others 1999c):

- Determining the foraging strategy, food intake, and growth (g/d) for the fish and habitat cell in question, for the current day. The potential growth at a destination cell is determined by simulating how much food would be obtained and how much energy it takes to swim in the cell (Section IX.C).

- Projecting the fish's weight, length, and condition factor K that would result if the current conditions persisted for the number of days specified by "fishFitnessHorizon". The daily growth is multiplied by fishFitnessHorizon to determine the change in weight; the corresponding change in length and K are determined using the methods described in Section IV.C.

- Approximating the probability of survival over the fitness horizon by using the following equation, which estimates survival as the first moment of the logistic function of starvation survival vs. K (Section IX.D.5):

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

where K_t is the fish's condition factor 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 logistic curve parameters determined (within the code, from the user-provided parameter values) for the poor condition mortality function (Section IX.D.5). This equation causes 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, we set starvSurvival equal to the daily survival probability for K_t raised to the power "fishFitnessHorizon" whenever the difference between K_{t+T} and K_t is less than 0.001.

The term "fracMature" represents how close to the size of sexual maturity a fish would be at the end of the fitness time horizon. It is simply the length the fish is projected to be at the end of the time horizon divided by the parameter "fishSpawnMinLength" (defined in Section IX.A.6). This term induces a movement gradient toward sites with higher growth for fish that have not yet reached the size allowing them to spawn. (Note that we assume both sexes have the same length at sexual maturity, an assumption that may not be valid for many populations of salmonids.)

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 "unified foraging theory" literature (Mangel and Clark 1986). Smaller values of fishFitnessHorizon place less emphasis on food intake and avoiding starvation in movement decisions. Values of fishFitnessHorizon of 5-10 d caused 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.

To our knowledge, only two studies address the issue of fitness time horizons. Bull and others (1996) used a model similar to ours and assumed overwintering juvenile salmon used the remaining winter period as a time horizon. Thorpe and others (1998) proposed using the duration of various salmonid life stages as time horizons. If we follow the lead of this literature and assume 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. We use "fishFitnessHorizon" equal to 90 d and include evaluation of alternative assumptions in our research priorities (Section X.C.3).

Move to Best Destination—The fish identifies the cell that has the highest value of the expected maturity fitness measure and then moves there. We do not limit movement by territory size or otherwise restrict the number of fish that can be in a cell. When a fish moves into a cell, the resources it uses are subtracted from those available for subsequent fish (Sections III.D; III.G.2). These resources may include one of the two kinds of food and velocity shelter. Because fish may move into a cell even when none of these resources remain available to it, its consumption of them is zero.

IV.C. Feeding and Growth

The model's methods for determining the daily growth (change in weight, g/d) that a fish would obtain in a specific habitat cell are used both in the daily movement decision and to determine growth once a fish has moved. Growth is determined by using the foraging and energetics methods described in Section IX.C. Food intake and growth depend on fish size, habitat conditions, and food availability in the cell. Growth can be negative, a situation common in nature (Railsback and Rose 1999).

We do not specify the exact kinds of food consumed by fish, but our feeding formulation and parameters generally represent invertebrate food. Even though

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the model assumes small fish are vulnerable to predation by adult trout (Section IX.D.7), feeding studies at the Little Jones Creek study site indicate that fish make up a small part of the trout diet. Therefore, we do not represent piscivory in the feeding model.

Unlike previous individual-based stream trout models, we assume that fish compete with each other for the available food instead of for feeding space. We assume each cell has a certain amount of food produced in it each day and the food available to a fish in the cell is limited by the cell's food production and the amount of food eaten by other fish in the cell (Section III.G). In combination with our movement rules, this assumption makes fish density a property that emerges from food availability and mortality risks instead of being imposed by requiring territorial behavior.

Our model includes two alternative 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). We model drift food intake (Section IX.C.2) as a function of stream depth and velocity and fish length; intake peaks at an optimal velocity that is higher for larger fish. We model the effect of turbidity on drift intake, reducing intake as turbidity increases. Metabolic costs for drift feeding increase with water velocity, but use of velocity shelters reduces this cost. Actively searching for benthic food and food dropped into the stream from overhead is an alternate strategy that 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 and others 1998). We assume the energetic benefits of search feeding are mainly a function of food availability, with energetic cost depending on water velocity (Section IX.C).

For both of these strategies, we model the potential food intake and metabolic costs a fish would experience in a cell; the fish then selects the strategy that provides the highest net energy (which often can be negative). Following standard bioenergetics approaches, we assume growth is proportional to net energy intake.

From the daily growth, the model determines the changes in length and condition factor. No simple, realistic ways of modeling this have been established. We adopt the simplistic approach developed by Van Winkle and others (1996), but propose the development of alternative approaches that seem likely to be more realistic and in better accord with our modeling philosophy (Section X.A.3).

The method for calculating daily change in length we adopt from Van Winkle and others (1996) also uses their nonstandard definition of a condition factor, K, a unitless index of how much weight a fish has relative to its length. This condition factor can be considered as the fraction of "normal" weight a fish is, given its length. The value of K is 1.0 when a fish has a "normal" weight for its length, according to a length-weight relation input to the model. Fish grow in length whenever they gain weight while their value of K is 1.0. Condition factors less than 1.0 indicate that the fish has lost weight. In this formulation, condition factors greater than 1.0 do not occur.

Weight, length, and K are calculated in this way:

- The fish's weight is changed by the value of dailyGrowth (calculated using methods in Section IX.C; note that daily growth can be negative).

- The length of a healthy fish with the fish's new weight ("fishWannabeLength") is calculated from the inverted length-weight relation (with the same parameters used to initialize new fish, Section II.B):

$$fishWannabeLength = \frac{fishWeight}{fishWeightParamA}^{1/fishWeightParamB}$$

- If the fish's actual length is less than fishWannabeLength (indicating that the fish is not underweight), then its length is set to fishWannabeLength.

- If the fish's actual length is greater than fishWannabeLength (indicating the fish is underweight for its length), its length is not changed.

The new condition factor (unitless) is equal to the fish's new weight divided by the "normal" weight for a fish its length:

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

It is important to note several limitations of this formulation:

- It does not allow fish to store a high-energy-reserve condition. Fish will have a condition of 1.0 only on those days when daily growth is positive. Even if a fish has eaten well for many days in succession, its condition factor can only be as high as 1.0 and one day of negative net energy intake causes condition to fall below 1.0. This could be a serious problem where short periods of high food intake are common.

- 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, our model cannot predict the existence of unusually fat fish.

- The energetics of reproduction are not considered (Section IX.A). We do not model how the need to store energy for gonad development affects length and weight, nor how the loss of gonads in spawning affects weight.

Our research objectives include addressing these limitations (Section X.A.3).

IV.D. Survival

Our survival simulations determine, each day, which fish die from what causes. Mortality sources are modeled using survival probabilities. (By "mortality source" we mean the individual processes we model that can cause mortality, e.g., predation, poor condition, high temperature.) Survival probabilities are the daily probability of not being killed by one specific mortality source. Survival of multiple mortality sources can be calculated simply by multiplying together the survival for each individual source. The mortality sources we model are:

- High temperature
- High velocity (representing exhaustion and inability to maintain position)
- Stranding (including predation risk associated with extremely shallow habitat)
- Spawning (occurring only to adults on the day they spawn)
- Poor condition and starvation
- Predation by terrestrial animals
- Predation by fish.

The survival probability functions used to determine whether a fish lives or dies depend on the fish's state (length, condition) and its habitat (depth, velocity, temperature) (Section IX.D).

Understanding and calibrating mortality in the model requires that we evaluate each potential mortality source separately; if we calculated one daily overall survival probability for each fish each day, we would not be able to attribute mortality to any particular source (Section VI.B). Therefore, we treat each mortality source as independent from the others. For each mortality source,

we obtain the survival probability from the fish's mortality methods (Section IX.D) and obtain a random number from a uniform distribution between zero and one. If the random number is greater than the survival probability, then the fish dies as a result of the mortality source.

V. Redd Model

Redds are the nests laid by spawning salmonids. A redd is modeled as one object. We do not track individual fish until they emerge from redds. The model keeps track of the number of eggs remaining alive in each redd. Characteristics of the spawner determine a redd's species and number of eggs. The eggs develop each day at a rate that depends on temperature. We do not explicitly simulate the changes in fish morphology and life stage that occur in the redd—all fish in a redd are considered eggs until they emerge as age-0 fish.

Redds are modeled as having four daily actions—survival, development, emergence, empty redds—that determine the number of age 0 fish produced. Scheduling of these actions is discussed in Section VI.C.

V.A. Survival

Eggs 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 differ from survival probabilities because they determine, for each redd on each day, the fraction of eggs that survive one particular kind of mortality. This fraction is then multiplied by the number of eggs in theredd to determine how many eggs survive. The number of eggs surviving is rounded to an integer.

Most redd survival functions are straightforward functions of the daily depth, velocity, and temperature in the redd's habitat cell (Section IX.E), but mortality due to "superimposition" is less straightforward. Superimposition can be important if spawning habitat is very limited compared to the number of spawners, or fish superimpose on existing redds more frequently than predicted by habitat availability alone (Essington and others 1998).

We track how many eggs die of each mortality source by applying each redd survival function individually, updating the number of surviving eggs after each function is applied (Section VI.C).

V.B. Development

To predict the timing of emergence, the developmental status of a redd's eggs is updated daily. We use the fractional development approach of Van Winkle and others (1996). The model accumulates the fractional development of the redd 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 reddDailyDevel. When fracDeveloped reaches 1.0, then the eggs are ready to emerge.

The daily value of reddDailyDevel is determined using this equation:

$$reddDailyDevel = reddDevelParamA + (reddDevelParamB \times temperature) + (reddDevelParamC \times temperature^{2})$$

In the absence of values specific to cutthroat trout, we use the rainbow trout parameter values of Van Winkle and others (1996; *table 4*). A simple degree-day model for cutthroat (emergence occurring 430 to 560 degree-days after spawning) was tested by June (1981). June observed the number of degree-days between spawning and emergence at his field site to range from 475 to 600, and the 430-560 model predicted emergence within 12 days.

Table 4—*Parameter values for egg development rates.*

Parameter	Definition	Units	Value
reddDevelParamA	Constant in daily redd development equation	none	-0.000253
reddDevelParamB	Temperature coefficient in daily redd development equation	$(°C)^{-1}$	0.001340
reddDevelParamC	Temperature squared coefficient in daily redd development equation	$(°C)^{-2}$	0.0000321

We compared this degree-day approach to the equation and parameters of Van Winkle and others (1996), using temperatures measured at the lower Little Jones Creek study site in 1998 and assuming spawning on May 8. The Van Winkle and others equation predicted emergence on July 5 after 614 degree-days; this was 4 days after the threshold of 560 degree-days was met. It appears that these two methods produce similar results.

V.C. Emergence

When eggs in our model are fully developed, they "emerge" from the redd as new fish. (Real trout actually pass through a life stage known as "alevin" before emerging; however, we do not distinguish between eggs and alevins in the model.) New fish emerge over several days. The following steps are used to determine how many fish emerge each day.

V.C.1. Emergence Timing

We assume that no new fish emerge until the day upon which eggs are fully developed (the day when fracDeveloped reaches 1.0), and then the fish emerge over a period of several days after this. Causing emergence to occur over several days represents 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 (but artificial) way to spread emergence over about 9 days, we assume that the fraction of remaining eggs that become fish on each day is 0.1 the first day, 0.2 the second day, 0.3 the third day, etc. until all fish have emerged.

V.C.2. New Fish Attributes

For each egg that emerges as a new fish, 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, assuming 50 percent of fish are each sex.
- The length of each individual fish is assigned from a random normal distribution with mean equal to the parameter reddNewLengthMean and a variance equal to the parameter reddNewLengthVar.
- Weight is calculated from length, using the same method used to create initial fish (Section II.B).

We estimate length parameters for newly emerged fish *(table 5)* from a study of coastal cutthroat in Washington (June 1981). This study measured lengths of newly emerged fry found in a downstream trap. A few of these had lengths between 2.4 and 2.7 cm, but most were between 2.7 and 3.0 cm.

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Table 5—*Parameter values for size of newly emerged fish.*

Parameter	Definition	Units	Value
reddNewLengthMean	Constant for new fish length equation	cm	2.8
reddNewLengthVar	Variance in length of newly emerged fish	cm^2	0.04

From Elliott (1994), we assume that fish emerging from a redd vary slightly, but perhaps significantly, in size. This variation in starting size gives larger fish an advantage in dominance that is likely to persist and grow over time. Elliott (1994) observed a coefficient of variation of 0.07 in length at emergence for brown trout at several sites. We adopt this value by converting it to the variance in length (parameter reddNewLengthVar, cm^2); with a coefficient of variation of 0.07 and a mean length of 2.8 cm, reddNewLengthVar is 0.04 cm^2.

We assume, by assigning weight this way that all fish are of normal condition when they emerge. Alternative assumptions (e.g., that initial condition is a random variable) are easily implemented, but we know of no basis for such assumptions.

Previous models (Railsback and others 1999a, Van Winkle and others 1996) assumed a relation between the size of a spawning female and the size of its eggs and, therefore, the emergence size of its offspring. This variation may be very 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. We assume, however, that variation in new fish size with spawner size is not important in resident cutthroat trout.

V.D. Empty Redds

Then 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.

VI. Model Schedules

The schedule in which events occur is a key factor determining the outcome of individual-based models. This section defines the order in which trout model actions occur.

We followed several guidelines in defining the schedule. In general, an action is placed in the schedule before any others that might be affected by it. The schedules for imposing mortality sources consider the fact that placing a mortality source earlier in the schedule makes it slightly more likely to cause mortality (a mortality source cannot kill a given fish on a given day if a preceding mortality source does so first). Therefore, we schedule widespread, less random mortality sources (e.g., high temperatures, high velocities) first; survival probabilities for these sources tend to be either negligible (1.0) or very low when some mortality event occurs.

In this section, we consider the computer implementation of the model by scheduling the "observer" actions that allow us to observe the model's state as it executes. This computer implementation is included because users of the model must understand how the observer schedule affects the model's output.

VI.A. Habitat Actions

Characteristics of individual habitat cells (depth, velocity, temperature, turbidity, and food availability) are updated daily. The physical habitat is updated first because subsequent fish and redd actions depend on that day's habitat conditions.

VI.B. Fish Actions

Fish actions are scheduled before redd actions because one fish action (spawning) can cause mortality of eggs or fish in redds by superimposition. This order means that new fish emerging from a redd are not simulated as fish until the day after emergence.

The four fish actions in the model are conducted in the following order: spawning, movement, growth, and survival. Actions are carried out one fish at a time, from the longest to the shortest individual. Each action is conducted for all fish before the next action is begun.

We schedule spawning as the first fish action because we assume spawning is the primary activity of a fish on the day it spawns. Spawning also is scheduled before survival because a fish's survival probability is reduced when it spawns.

Movement is scheduled as the second fish action each day to allow fish to move in response to each day's new habitat conditions before feeding and survival simulations. Movement strongly affects both growth and survival. Movement decisions are based in part on survival probabilities, which vary with fish size, and we base movement decisions on survival probabilities evaluated for the fish's current size (before the current day's growth, which depends on its movement destination). This assumption can be considered a shortcut that introduces an error expected to be negligible in almost all cases.

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

Fish survival includes evaluation of a number of mortality sources, and the number of fish killed by each mortality source depends on the order in which survival probabilities for each source are evaluated.

The schedule of fish actions has subtle implications for testing the model software. Processes that affect fish movement and growth (e.g., food intake, swimming costs) can produce different results when executed during the movement action than they do when executed during the growth action. This is because these actions depend on how many other fish are in the fish's cell, which changes as movement is executed. The availability of food and velocity shelters decreases as more fish are added to a cell during the movement action. For this reason, re-calculating net energy intake for a fish after the movement action is completed would produce a result that was not valid at the time the fish made its movement decision. Likewise, mortality risks evaluated during movement will differ slightly from those used in the survival action because the fish has acquired its daily growth after movement and before survival actions, and survival probabilities depend on fish size. Software tests must consider the availability of food and velocity shelters, and the fish's size, that occurred at the time each fish made its movement decision.

VI.C. Redd Actions

Redd actions occur last each day because redds do not affect either habitat cells or fish (with the exception of creating new fish).

Three model actions affect redds: survival, development, and emergence. Survival is scheduled first because the number of fish emerging is a function of survival. Also, if emergence were scheduled before redd survival, new fish would be subject to no mortality (either as fish or as eggs) on the day of their emergence. Development is scheduled before emergence because we assume new fish emerge on the same day egg development is complete (if development were scheduled after emergence, then fish would begin to emerge the day after development was complete).

Redd survival includes several separate egg survival probabilities; the least random sources (dewatering, scouring) are first, and the most random (superimposition) is last.

VI.D. Observer Actions (Model Outputs)

We schedule observer actions as the last of the daily model actions. This means that the model's graphical and file outputs represent the state of the model after all the habitat, fish, and redd actions have been completed for a time step. Intermediate states of the model (e.g., the number of eggs in a redd after some, but not all, survival functions have executed; the size of a fish at the time it made its movement calculations but before its simulated growth; the food availability in a cell before all its fish moved into it) can only be observed by specifically telling the software to save the desired values.

Our software allows the model user to identify and "kill" individual fish via the graphical user interface. This observer-induced mortality (not otherwise described in this document) occurs during the observer actions at the end of a time step.

VI.E. Complete Schedule

The complete schedule of event execution in the model follows this order:

1. Habitat Actions: Update flow, depth, velocity, temperature of cells

2. Fish Actions

   a. Spawning

   b. Movement (move fish in order of decreasing dominance)

   c. Growth

   d. Survival

      i. High temperature

      ii. High velocity

      iii. Stranding

      iv. Spawning

      v. Poor condition

      vi. Terrestrial predation

      vii. Aquatic predation

3. Redd Actions

   a. Survival

      i. Dewatering

      ii. Scouring

      iii. Low temperature

      iv. High temperature

      v. Superimposition

   b. Development

   c. Emergence

4. Observer Actions: Model outputs

VII. Calibration

Calibration has the objectives of testing, demonstrating, and improving the model's ability to reproduce observed phenomena. Calibration includes changes in parameter values and, possibly, revision of the model formulation. Calibration occurs in two major phases:

- Individual components of the model formulation (e.g., feeding and growth methods) are tested and calibrated as they are designed. In this document, discussion of such calibration is included in the sections describing individual formulation components.

- The full model is calibrated after all model components have been designed and calibrated individually, the entire model has been implemented in computer code, and the code checked thoroughly.

This section discusses full-model calibration methods that are useful only after individual model components have been tested and calibrated. Calibration to date has included empirically fitting food availability and survival probability parameters, and testing of the model's ability to simulate movement and habitat selection realistically.

Calibration of complex models requires a systematic approach. Because our model is designed to simulate the population level changes that result from individual fish behavior, the actions of individual fish must be calibrated before there can be any chance of successfully calibrating population-level characteristics. On the other hand, there are feedbacks from population-level characteristics to individual actions (e.g., when populations are high, growth of many individuals may be lower). In addition, individual characteristics may not be reflected in population-level statistics (e.g., many individual fish may have growth rates much less than the observed population average because they do not survive until population observations are made). Considering such complexities, we recommend the following approach to calibration:

- Calibrate individual and short-term responses before attempting to calibrate population-level, inter-annual responses. The ultimate goal of the model is to predict population responses to environmental changes like altered discharge regimes, but there are an infinite number of ways to calibrate the model so that it reproduces observed population-level responses.

- Focus calibration on underlying processes driving individual fitness instead of using "brute force" adjustments to match observed data. Models that produce realistic behavior and population responses as patterns that emerge from simple rules are more powerful than models where realistic behaviors are imposed by inflexible rules. For example, the relative abundance of two species in a model should emerge from the fitness of individuals of each species (e.g., fish that emerge from redds earlier may have an advantage over late-emerging fish because the former begin growing sooner) rather than from different imposed mortality rates that produce observed differences in abundance.

- Establish appropriate calibration criteria, which vary among processes and need not always be numerical. In general, reproducing observed patterns in the response of fish to events is more useful than exactly reproducing observed data (Railsback 2001).

- At each level of calibration, identify parameters (or equations) that appear most appropriate to change via calibration. These are generally parameters or equations that have strong effects on the model action being calibrated and are more uncertain.

VII.A. Individual Actions

The actions of individual fish and redds should be calibrated first. We identified the following criteria for fitting individual fish and redd actions to observations, and we identified the parameters that should be adjusted first during calibration. This section also describes calibration conducted to date.

VII.A.1. Fish Spawning

The predicted date of spawning can be compared to observed spawn timing (which is rarely known precisely). The habitat cells where model redds are placed can be compared to observed spawning habitat preferences. The models for timing and location of spawning are simple and closely constrained; they should require little if any calibration if the parameters were selected accurately.

VII.A.2. Fish Growth and Survival

Although pre-calibration values for important and uncertain food availability and survival probability parameters were estimated during model development (Section IX.C.9, Section IX.D.8), calibration of the full model is required to obtain realistic growth and survival of model trout. The preliminary growth and survival calibration described here produced food and survival parameters that have been used for a number of long-term simulation experiments. To calibrate food availability and predation risks at our Little Jones Creek study site, we developed the following criteria.

Calibration was conducted over a 75-day period from July 19 to October 2, 1998. The lower study site was used. We estimated the initial relative abundances of age classes *(table 6)* by using field data from July 1999. We doubled the total abundance of fish observed in 1999 to reflect data from three previous censuses of Little Jones Creek by other workers.

The number of age 0 fish could not be estimated in July because some members of this age class were not large enough to census. Consequently, we calibrated survival for age 1 and older fish and then used the model to estimate the July 19 abundance of age 0 fish.

The target ending (October 2) population characteristics *(table 7)* were estimated from field observations collected at the Little Jones study site at the end of September 1999, supplemented with rainbow trout data from a site on the Tule River, Sierra Nevada, California, from which field data for 11 years are available (Studley and others 1995, Railsback and Rose 1999). The Tule site (upstream of the Tule River diversion dam) is roughly similar to Little Jones Creek in habitat type and structure, but has higher summer temperatures and brown trout that compete with the rainbow trout.

The ending average lengths for each age class were taken from the Little Jones Creek field data. The calibration targets for numbers of trout were developed from both Little Jones and Tule River data. The apparent mortality rates observed in Little Jones Creek in 1999 were quite low, whereas the Tule River data had average summer mortality rates (for a time period roughly equal to our 75-day calibration period) of 40 percent for age 1 and 2 trout.

Table 6—*Initial population characteristics for calibration.*

Age, y	Number	Mean Length, cm	Variance in Length, cm
0	unknown, > 450	50.0	0.67
1	50	11.4	1.69
2 and above	20	16.9	7.56

Table 7—*Ending population characteristics used as calibration targets.*

Age, y	Number	Mean Length, cm
0	450	6.9
1	40	12.8
2 and above	15	19.0

Table 8—*Calibration results.*

Output	Run 1	Run 2	Run 3	Run 4	Run 5	Mean	(SD)
Age 0 abundance	472.0	446.0	451.0	429.0	444.0	448.0	(16.0)
Age 1 abundance	39.0	35.0	38.0	39.0	32.0	37.0	(3.0)
Age 2+ abundance	18.0	15.0	17.0	19.0	17.0	17.0	(1.0)
Age 0 length	6.4	6.6	6.6	6.6	6.7	6.6	(0.1)
Age 1 length	12.9	13.0	13.5	12.4	13.1	13.0	(0.4)
Age 2+ length	18.6	18.2	18.8	18.5	18.2	18.5	(0.3)

We calibrated growth (change in length) for age 1 and older fish by adjusting the food availability parameter that represents the concentration of drift food in the water column (habDriftConc). Because many age 0 fish used the active searching feeding strategy, we next used the density of search food (parameter habSearchProd) to calibrate age 0 growth. We assumed that aquatic predation is the most important (along with poor condition) and least certain mortality source for age 0 trout. The parameter mortFishAqPredMin was therefore used to calibrate age 0 survival. Similarly, we assumed that terrestrial predation is the most important and least certain mortality source for age 1 and older fish and used the parameter mortFishTerrPredMin for calibration of survival for these age classes.

We did not attempt to calibrate survival and growth precisely, but we did try to ensure that rates and causes of mortality and growth rates were reasonable. The calibration process produced these values of the calibration parameters:

- habDriftConc: 1.50E-10
- habSearchProd: 7.0E-7
- mortFishAqPredMin: 0.997
- mortFishTerrPredMin: 0.99

Terrestrial predators account for about 40 percent of mortality of age 0 fish in the calibrated model. The rest of the mortality was evenly spread among aquatic predation, stranding (which includes the extreme predation risk in shallow water), and starvation.

We conducted five replicate model runs (initialized with different random number seeds; *table 8).* These can be compared to the calibration targets in *table 7.*

VII.A.3. Fish Movement

Because moving to different habitat is a primary way that stream fish adjust to changing conditions, testing the model's ability to represent movement realistically is a key step in calibration. Movement, survival, and growth are closely linked: survival and growth rates are the factors that determine how fish move, and where fish move affects their survival and growth rates. After we conducted the calibration of survival and growth, we tested the model's simulation of movement and habitat selection by trout. We identified six observed patterns of shift in habitat by trout in response to known stimuli; the model reproduces all of these patterns. This test is documented in a separate publication (Railsback and Harvey 2001).

VII.A.4. Redd Survival

Data allowing calibration of survival rates of eggs in individual redds will rarely be available. Calibration may be limited to making sure survival rates are reasonable for periods when redd mortality factors can safely be presumed to be low.

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VII.A.5. Redd Development and Emergence

Because redd development rates are dependent only on temperature, full-model calibration is not needed (Section V.B).

VII.B. Short-term Population Responses

Long-term population predictions are likely to be inaccurate if predicted responses to short-term events are not realistic. We recommend the following short-term events be simulated and the model calibrated to reproduce observed responses.

VII.B.1. Seasonal Changes in Habitat Use, Growth, and Survival

Several changes in habitat use patterns with season and fish size are well documented (PG&E 1994, Vondracek and Longanecker 1993). These patterns include use of increasing depths in the first year of life and selection of lower velocities in winter. The model has been shown to predict changes in habitat selection with seasonal changes in temperature and day length (Railsback and Harvey 2001), but the magnitude of these habitat shifts have not been calibrated.

The model's seasonal patterns in habitat use, growth, and survival will be highly dependent on the assumptions made about how food availability varies. (Currently, we assume no seasonal variation in food availability.) One way to match such seasonal patterns is to adjust food availability by season or temperature, one of our research priorities (Section X.B.4).

VII.B.2. Redd Scouring and Temperature-related Mortality

There is strong evidence that scouring of redds and temperature-related mortality of incubating eggs are relatively common and have major consequences for trout populations. Historic data on recruitment success may be useful to calibrate the model to reproduce these important short-term events.

VII.C. Long-term Population Responses

A primary objective of the trout model is to predict long-term population-level responses to changes in flow and other conditions. These responses should be addressed in calibration only after it has been determined that simulations of individual actions and short-term responses are realistic.

As with previous calibration levels, it is important to ensure that the model reproduces observed processes and relations, not just observed outcomes like abundance or average growth. For example, matching observed (or literature-based) effects of driving variables like flow and temperature on predicted population should take priority over simply matching long-term mean population measures.

The model should not be calibrated using field data strongly affected by processes not included in the model. Our model currently does not simulate emigration or immigration, stocking, or angler harvest; caution should be used when attempting calibration to data from periods when these processes may be important.

VII.C.1. Redd Numbers and Incubation Success

Because long-term patterns of spawning, redd numbers, and the number of fish produced per redd are difficult to observe, direct calibration of the number and success of redds is unlikely. In cases where redd counts are available from multiple years, calibration could include testing the model's ability to predict trends between redd numbers and spawner abundance or flow. Because of the difficulty of field observations, we expect redd success can normally be calibrated only as one of the factors driving the abundance of age 0 trout.

VII.C.2. Long-term Abundance, Growth, and Relative Abundance

Once simulations of individual behavior simulations appear reasonable, long-term growth rates should be calibrated by adjusting the food availability

parameters, similar to the process of calibrating individual fish actions. (Small differences in calibration of daily growth of individuals can add up to large errors in long-term average growth of a population.) Keep in mind that survival rates affect growth because remaining individuals will have access to more food when populations are low, and size-dependent mortality (e.g., higher starvation or predation mortality in smaller individuals) changes the population-level growth rates.

Long-term abundance is a cumulative result of survival rates (and reproduction rates). Because starvation can be an important mortality source, abundance cannot be calibrated precisely until feeding and growth simulations are relatively accurate. To calibrate non-starvation survival, we recommend using the parameters controlling aquatic predation risk (mortFishAqPredMin) and terrestrial predation risk (mortFishTerrPredMin) because these are generally less certain than other risk factors (high temperature, high velocity, stranding, and spawning). Variation in mortality with fish size can be used to guide calibration of these parameters; aquatic predation affects only small fish.

VIII. Habitat Data Collection Methods

Field data to depict habitat for this individual-based model should differ from the data typically used for habitat assessment models like PHABSIM. This is because the objective of habitat modeling in the IBM is to provide a map of habitat relevant for the model's daily time step and spatial processes, whereas PHABSIM characterizes hydraulics in detail across a few selected transects. In general, habitat data for the trout model should be collected at more transects and fewer points across each transect than typically used for PHABSIM. Field data include cell size and location, depth and velocity at several flows to calibrate a hydraulic model, availability of spawning gravel and velocity shelter, and distance to hiding cover. In addition, water surface elevations at high flows help calibrate the hydraulic model.

The following guidelines are intended to help modelers familiar with PHABSIM field techniques collect data appropriate for our trout IBM.

VIII.A. Reach Location and Length

The selection of a stream reach for modeling should consider the purpose of the modeling study. If the model is intended for research purposes, then the study design (e.g., testing the model against field observations, comparing predictions among different habitat types) should be a primary consideration in reach selection. Models intended to provide management information may best use reaches that represent habitat of the whole river, but should also include any habitats known to be important to the fish population (e.g., unique spawning areas or sites with very high fish densities).

We do not yet have the experience to provide specific guidance on appropriate reach lengths. Considerations include how important fish movement is expected to be, locations of barriers to movement, and how much habitat varies along the river. Longer reaches with more fish require more computer time to execute, but this should not be considered a limitation.

VIII.B. Transects and Longitudinal Cell Boundaries

Our approach for defining cell boundaries in the longitudinal (upstream-downstream) direction is simpler than that of PHABSIM. In PHABSIM, transects are the lines across the stream where depths and velocity are measured to calibrate the hydraulic model. The cell borders between transects are defined by the "transect weighting factor," the percent of the distance to the next upstream transect. Instead, we treat a transect as a row of cells across the river and directly measure the location of the boundary between each pair of adjacent transects.

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Unlike PHABSIM conventions, we also measure the upstream and downstream extent of the cells on the upstream and downstream ends of the study reach. We measure all these distances from downstream to upstream, with zero being at the downstream end of the cells represented by the first (most downstream) transect.

The transects and their boundaries are placed to capture the upstream-downstream variation in habitat, using the following criteria:

• Represent all the habitat types that are common in the reach; include the full range of variation in habitat.

• Include habitat types known to be important to fish even if they are rare; for example, areas with high concentrations of large woody debris.

• Do not exclude common habitat types even if they are not expected to be important to fish.

• Do not place transects closer together than about 1 meter, to avoid cell boundary effects in simulations. There is no upper limit due to modeling considerations on distance between transects.

The frequency of transects should reflect the longitudinal physically heterogeneity of the habitat, e.g., riffles with consistent depth and substrate may be represented by one or two transects.

VIII.C. Lateral Cell Boundaries

The best approach to placing cells across transects for this model does not follow standard PHABSIM methods. The PHABSIM approach was adopted from stream gaging techniques without giving adequate consideration to consequences for habitat modeling (Railsback 1999). In PHABSIM, "stations" (points where bed elevation, depth, and velocity are measured) are usually spaced evenly at a minimum of 20 points across the channel; cell boundaries are then automatically placed halfway between each station. Instead, we use fewer, less evenly spaced cells.

The goal in placing lateral cell boundaries is to make variation in habitat (depth, velocity, velocity shelters) low within each cell, but high among cells. It helps to remember that because the fish model assumes the depth and velocity are uniform within each cell, it sees a transect as a series of level cells *(fig. 2)*.

The cell boundaries are the points along the transect where, in the model, the bottom elevation changes; the task in the field is to determine where these boundaries should be. They should be measured and recorded in such a way tha they can easily be relocated at different flows. These distances are entered into the model as distances across a transect from left bank to right bank, facing upstream, so it helps avoid errors to measure them in the same direction. The distance of each boundary from the end of the transect must be recorded. In addition, a bottom elevation representative of the cell average should be measured. In many cases, this representative elevation will be taken near the cell's center (halfway between the boundary points), or the average of the elevations at each of the cell's boundaries could be used. However, if the cell's bottom elevations do not vary gradually or consistently (e.g., if they contain large boulders or the thalweg), then the representative bottom elevation may need to be measured at some other point.

Figure 2 —Transect depicting cells with uniform depth. Left to right is the channel, looking upstream.

The following criteria should be used to define cell boundaries:

- On at least the lowest bank of the river, the first cells should be high enough to include some overbank habitat so that the model includes refuge habitat when flows are above bank-full.

- Cell boundaries should be placed wherever there are significant, sudden changes in slope, depth, velocity, or substrate type across the transect. Where depth, velocity, and substrate type remain fairly uniform across the transect, there is no need to put cell boundaries close together—there is no recommended upper limit on cell width.

- Where habitat varies steadily across the transect (e.g., the bed has a constant slope so that depth and velocity steadily increase), cell boundaries should be relatively close together.

- Cell boundaries should not be less than about 1 m apart, to avoid undesirable boundary effects in the fish model. Cells should ideally be wider than 2 m to keep them large compared to the width of stream individual fish can search for drifting prey (Section IX.C.2).

- If there is a well-defined thalweg, or a local elevation peak, it is probably best to place the boundary between two cells on it. This way the maximum (or minimum) depths and velocities will not be modeled, but the averages conditions around them will be represented.

In the field, we find it useful to stretch a measuring tape across each transect then tie short pieces of surveyor's flagging onto the tape at the boundaries between cells. The pieces of flagging are easily moved along the tape as alternative cell boundaries are considered.

VIII.D. Depths and Velocities

To calibrate the hydraulic model, we need to measure water depths and velocities that represent each cell. These measurements should be made at a minimum of three different flows. The location where measurements are made should be recorded. It is not essential that the representative depth and velocity be measured at the same place each time they are measured at different flows, but doing so may avoid some potential calibration problems.

The velocity values should be mean column velocities. At water depths up to 1 m, velocity can be measured once at 0.6 of the depth below the surface; at higher depths, or in highly variable velocities, measurements should be made at 0.2, 0.6, and 0.8 of the depth and averaged.

The model bases all velocity-dependent calculations on the velocity's magnitude, not its direction. Therefore, all velocity measurements should be made with the meter facing directly into the cell's local flow direction, even if the cell's flow direction is not perpendicular to the transect. It is important to measure the velocity's magnitude in its prevailing direction; no negative velocities should be recorded. (For example, if a cell is in an eddy and its velocity is 10 cm/s in the upstream direction, it should be recorded as +10 cm/s.) It does not matter if the velocity direction in a cell changes among the several different flows used for calibration; the velocity magnitude in its prevailing direction should be measured in each case. This practice may make conventional hydraulic model "calibration" methods more difficult, but provides a more meaningful depiction of stream habitat. (Recording the angle of flow with respect to the channel's direction may help in calibrating the hydraulic model.)

The following are criteria for determining where to measure depth and velocity in habitat cells:

The overriding criterion is that the depth and velocity measurements need to represent the cell's average conditions. Eddies, obstacles, rocks, etc. should be avoided if they appear to cause unrepresentative measurements.

- For relatively simple, uniform cells it should suffice to measure depth and velocity at one point near the cell's midpoint.

- For complex cells, or cells containing a thalweg or local elevation peak, it may be best to measure depth and velocity at several places within each cell. For example, four measurements could be taken, one in each quadrant of the cell. These measurements would be averaged to represent the whole cell.

- For cells that are dry at the time of measurement, it is necessary only to measure a representative ground elevation for the cell.

VIII.E. High-Flow Water Surface Elevations

For most applications, the individual-based model will need to adequately represent hydraulic conditions at flood flows. It is often dangerous and difficult to measure the depth and velocity in each cell at high flows. However, calibration of such flows can be accomplished adequately by measuring only the water surface elevation at each transect. Therefore, water surface elevations (and flow rate) should be measured at several high flows, up to and ideally above bankfull flow. These measurements are especially important for studies where high flow effects on fish and redds are important.

VIII.F. Spawning Gravel Availability

The model determines where fish spawn by using a parameter representing the percent of each cell's area that has gravel substrate suitable for spawning. This parameter must be estimated in the field, using judgment of what constitutes usable spawning substrate. We make no attempt to rate the relative suitability of different gravels. These measurements may best be made at low flows because the substrate (especially in pockets behind obstacles) is more visible. There is no need for this parameter to be estimated to more than one significant figure.

VIII.G. Velocity Shelter Availability

The model's formulation to determine the net energetic benefits of feeding locations includes the assumption that fish in a velocity shelter have negligible energetic costs for swimming. This formulation uses a parameter representing the percent of each cell's area that offers velocity shelter for drift-feeding fish. Parameter values will be approximate, as velocity shelter availability cannot be measured precisely and varies with fish size and flow rate; estimates should be considered accurate to no more than one significant figure.

The following criteria can be used in estimating how much velocity shelter area is available in a cell:

- Area should be included as having shelter if there is turbulence offering the possibility of fish finding a spot with low velocity. All area with such possibilities should be included, not just the actual area with very low velocities. For example, all areas with large boulder substrate should be included. We assume the fish are much better at finding velocity shelters in such turbulence than we are.

- Velocity shelters can be provided by bottom topography and substrate as well as by large obstacles in the water column.

- Adjacent areas of slow water can also provide velocity shelters. A cell containing fast water that has an adjacent cell of slow water (e.g., along a steep, rough bank) should be considered to have velocity shelter along the side of the cell where the horizontal gradient in velocity occurs. (Our model assumes that a fish's cell is where it feeds, not necessarily where it shelters while waiting for food.)

- Areas where the mean cell velocity is low should not be included as velocity shelter. Shelters should be areas where velocities are significantly lower than the cell mean. (In the model, velocity shelters are unimportant in quiet cells like pools.) This means that a cell with very low velocity may provide velocity shelter for fish feeding in an adjacent high-velocity cell, but does not have velocity shelter itself.

- It may be best to measure velocity shelter availability at higher calibration flows because the availability of shelter can vary with flow. For example, in a pool at low flow there may be no velocity shelter areas with velocities substantially less than the cell's mean velocity because that mean velocity is very low; but velocity shelters may appear and be important at higher flows. Overestimating the availability of shelter at low flows and velocities does not cause major errors in model predictions (velocity shelters have little effect on results in cells with low velocity). Therefore, it is better to consider conditions under intermediate to high flows when evaluating velocity shelters.

- According to the model's formulation for metabolic costs, the energetic cost of swimming equals and exceeds standard respiration at swimming speeds of around 30 cm/s. Hill and Grossman (1993) also found that activity respiration was a negligible part of the energy balance at velocities at least up to 40 cm/s. Therefore, areas where local velocities are less than 30 cm/s clearly offer shelter if their velocities are also substantially lower than the mean column velocity. However, because it is unlikely that we can find the lowest velocity in a turbulent zone as well as a fish can, apparent shelters should not be excluded if we cannot measure velocities less than 30 cm/s there.

VIII.H. Distance to Hiding Cover

The daily probabilities of avoiding predation depend on the availability of hiding cover. The use of hiding cover appears to occur at spatial scales larger than our habitat cells: fish can hide using cover several meters away. Therefore, we evaluate cover for each cell as the distance (m) from the cell to the nearest available hiding cover, whether or not that cover is within the cell.

Because cells can be fairly big, there will be no single value for the "distance to hiding cover" parameter that accurately fits the whole cell. Therefore, we estimate this parameter by using the distance from the center of the cell to cover. It should not be estimated to more than one significant figure. Values of zero are acceptable, for example if the cell has ample wood or undercut banks.

The kinds of objects providing hiding cover are likely to vary among sites, and site-specific observations (especially using radiotelemetry) are useful for determining where fish hide. Possible cover types include:

- Undercut banks and boulders
- Cavities in the substrate
- Wood and brush
- Water that is deep or fast enough to provide concealment.

IX. Method Details

This section provides the formulation details for parts of the model that are too complicated to be explained in full in the preceding sections. The goal of this section is to unambiguously describe the model in sufficient detail for it to be implemented in computer code or otherwise reproduced.

IX.A. Criteria for Day of Spawning

Trout are assumed to spawn only on days when all of the following criteria are met (Section IV.A.1). The order in which these criteria are evaluated does not affect model results. These rules for determining when trout are ready to spawn force the model to reproduce observed spawning patterns.

IX.A.1. Date Window

Salmonids generally have well-defined 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 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 other age 0 fish. We allow fish to spawn only on days within a user-specified date window.

The date windows are input parameters with values estimated from the literature and site-specific field observations from the Little Jones Creek study site *(table 9)*. June (1981) used redd surveys to estimate the time of spawning in a mixed population of anadromous and resident coastal cutthroat in Washington. Spawning was observed from mid-January through mid-May, with most redds formed in March. The May redds were apparently from resident trout, as anadromous fish were not present. Limited spawning observations in Little Jones Creek in 1999 found evidence of spawning between early April and late May.

IX.A.2. Temperature Range

To match observed behavior, we limit spawning to within a range of daily mean temperatures. Conceptually, it makes sense that spawners would use temperature as a cue to predict seasonal changes and avoid temperature-induced egg mortality (Section IX.E). We define the maximum and minimum temperatures for spawning, using parameter values estimated from the literature by Van Winkle and others (1996) for rainbow trout *(table 10)*.

IX.A.3. Flow Limit

The maximum flow limit implements an assumption that fish will not spawn during high flows when the best spawning habitat is likely to be in river margins. Spawning during flood flow tends to place the redds at risk of dewatering mortality when flows drop. Because this parameter is highly site-specific and very difficult to measure, we estimate values for each model site *(table 11)*.

Table 9—*Parameter values for spawning date window.*

Parameter	Definition	Units	Value
fishSpawnStartDate	Date at which spawning season starts	(Day)	4/1 (April 1)
fishSpawnEndDate	Date at which spawning season ends	(Day)	5/31 (May 31)

Table 10—*Parameter values for spawning temperature range.*

Parameter	Definition	Units	Value
fishSpawnMinTemp	Minimum temperature at which spawning occurs	°C	8
fishSpawnMaxTemp	Maximum temperature at which spawning occurs	°C	13

Table 11—*Parameter values for maximum flow for spawning.*

Modeling site	Value of fishSpawnMaxFlow (m³/s)
Little Jones Creek- Lower	4
Little Jones Creek- Upper	4
Little Jones Creek- Tributary	2

Table 12—*Parameter values for age, length, and condition limits on spawning.*

Parameter	Definition	Units	Value
fishSpawnMinAge	Minimum age for spawning females	Years[1]	1.00
fishSpawnMinLength	Minimum length for spawning females	cm	12.00
fishSpawnMinCond	Minimum condition factor for spawning females	none	0.95

[1]An integer number of years.

IX.A.4. Steady Flows

We assume fish do not spawn when flows are unsteady because flow fluctuations place redds at risk of dewatering or scouring mortality. We adopt from Van Winkle and others (1996) the criterion that fish spawn only if daily flow has changed less than 20 percent from the previous day. We define this criterion with the parameter "fishSpawnMaxFlowChange" (unitless), which we give a value of 0.20.

IX.A.5. Female Spawners

Our model does not track any affect male fish may have on the spawning process. Therefore, we conduct the spawning simulations only for female fish.

IX.A.6. Minimum Length, Age, and Condition

Because we do not explicitly simulate the bioenergetics of reproduction, we use fish length, age, and condition to predict energetic readiness to spawn. Minimum values of these characteristics *(table 12)* 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 number of years (following our convention for fish ages; Section I.C.4). We use 1 year for this parameter in the Little Jones Creek model. (Spawning in age 1 stream trout is rare but can occur.)

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 movement decisions; Section IV.B.2.) This length is likely to vary among sites. We estimated parameter values for the Little Jones sites from site-specific observations and the literature. June (1981) observed spawning marks in nine resident coastal cutthroat trout and estimated their length at spawning. Five of these fish spawned at age 2, at lengths of 12.0 to 14.5 cm. These observations indicate a minimum spawning length of about 12 cm.

A fish's condition factor (Section IV.C) must exceed the minimum condition factor parameter fishSpawnMinCond (unitless). Keeping in mind our non-standard definition of condition factor (Section IV.C), our growth formulation that makes it impossible that condition is equal to 1.0 on any days when fish did not obtain at least as much energy as expended for respiration, and that we do

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not simulate the bioenergetics of reproduction, we assume that fish do not spawn unless they have a condition factor near, but not equal, to 1.0.

IX.A.7. Not Spawned This Season

We assume trout do not spawn more than once per annual spawning season. We give the fish a variable "dateLastSpawned." If this date differs from the current date by a number of days less than the duration of the spawning date window, then the fish cannot spawn. When new fish are created, they are assigned a value of dateLastSpawned so that this criterion does not prevent any fish from spawning once in the first spawning season of a model run.

IX.B. Spawning Habitat Suitability

The spawning habitat selection method includes suitability factors for depth and velocity (Section IV.A.2). We interpolate a depth suitability factor (spawnDepthSuit; unitless) from the values in *table 13*. These values provide a simplified PHABSIM-type depth criteria curve *(fig. 3)*, 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.

A velocity suitability factor (spawnVelocitySuit; unitless) is interpolated from the values in *table 14*, which produces the function shown in *figure 4*. These values were estimated from a collection of brown trout spawning criteria (PG&E 1994). The number of points in this relationship is fixed at six.

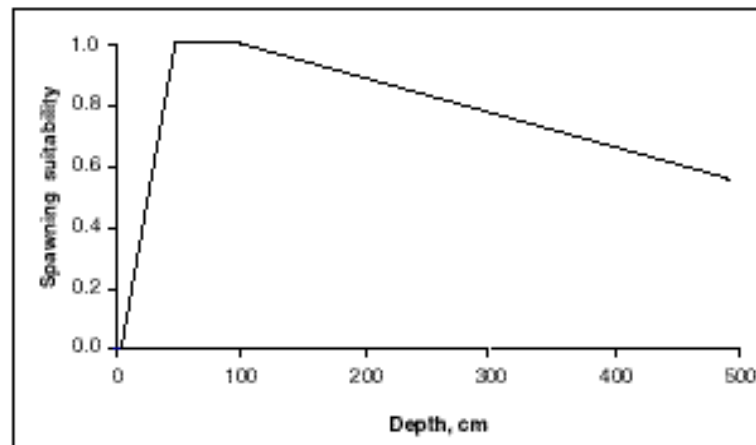**Figure 3** —Spawning suitability function for depth.

Table 13—*Parameter values for spawning depth suitability.*

Parameter Name	Depth (cm)	Parameter Name	spawnDepthSuit
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

IX.C. Fish Feeding and Energetics

The feeding and energetics methods determine the net energy benefits (joules of food energy per day available for growth) and growth (grams of fish mass per day) a fish would obtain if it were in a specific habitat cell. These methods are used both to evaluate potential destinations during movement (Section IV.B) and to simulate growth (Section IV.C).

The energetics methods are a simplified version of widely used fish bioenergetics models (Hanson and others 1997). Net food energy benefits of a site are equal to the fish's food intake (a function of food availability, depth and velocity, and fish size), minus respiration costs (a function of fish size, temperature, and swimming speed). Intake and costs differ between two foraging strategies: stationary drift feeding and active searching for food. Food availability can be limited by the consumption of food by other fish in a habitat cell. We assume fish select the more profitable of these two strategies. This approach is modified from that of Van Winkle and others (1996).

Sections IX.C.1 through IX.C.4 describe input to the net energy intake and growth calculations, which are detailed in Section IX.C.5. Parameter estimation and calibration for food intake and growth are discussed in Section IX.C.6.

IX.C.1. Activity Budget

Energy intake and costs differ between feeding versus resting fish. To avoid the need for sub-daily simulations, we parameterize the fish's daily activity schedule. Energetic calculations are based on hourly energy rates (j/h), and the daily energy totals depend on how many hours are spent feeding versus resting.

We simply assume that the modeled fish spend all daylight hours feeding. Hill and Grossman (1993) observed that rainbow trout in a small stream spent 98
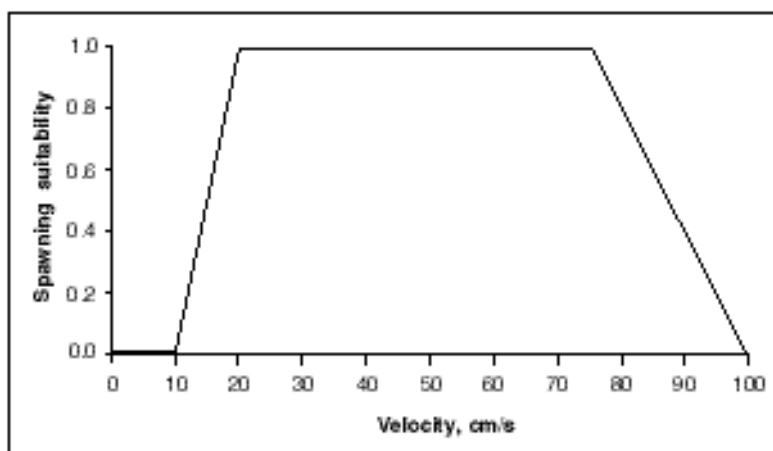

Figure 4 —Spawning suitability function for velocity.

Table 14—*Parameter values for spawning velocity suitability.*

Parameter Name	Velocity (cm/s)	Parameter Name	spawnVelocitySuit
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

percent of daylight (including dusk and dawn) feeding, except that no feeding occurred at temperatures below 2 °C. We include 1 hour before sunrise and after sunset in the feeding period. Consequently, we calculate the time spent feeding as:

$$feedTime\ (h/d) = daylength + 2;\ if\ temperature$$

$$< fishMinFeedTemp,\ then\ feedTime = 0.$$

This assumption is undoubtedly inaccurate for Little Jones Creek, where nocturnal activity and diurnal changes in activity have been documented (Harvey and others 1999). However, a more detailed depiction of activity budget would significantly complicate the model. (A strategy for doing so is outlined in Section X.A.4.) At this early stage in model testing we choose to use the simpler formulation.

The input parameter fishMinFeedTemp is a temperature threshold below which trout do not feed. Using the observations of Hill and Grossman (1993), we use a value of 2 °C for this parameter. Temperatures this low have not been observed in Little Jones Creek.

IX.C.2. Food Intake

Drift Feeding Strategy—Drift feeding fish wait and capture invertebrates as they are carried within range by the current. Our drift feeding energy intake formulation is modified and simplified from that of Van Winkle and others (1996), which was based largely on the work of Hill and Grossman (1993), Hughes (1998), and Hughes and Dill (1990). This literature shows clearly that prey items at greater distance from a fish are less likely to be captured, and the distance over which fish can capture food increases with trout size and decreases with water velocity. Unlike previous models, we include the negative effect of turbidity on the distance over which trout can see and capture prey (Barrett and others 1992). Turbidity varies dramatically in streams we study, and incorporating its effects on trout feeding is fairly straightforward. To avoid additional complexity in the model, we currently neglect the effect of prey size on capture probability.

We assume drift-feeding fish capture all food items that pass within a "capture area"—a rectangular area perpendicular to the current, the dimensions of which depend on depth, velocity, fish size, and temperature. A fish's intake per hour is calculated as the mass of prey passing through the capture area:

$$driftIntake\ (g/h) = habDriftConc\ (g/cm^3) \times velocity\ (cm/s)$$

$$\times captureArea(cm^2) \times 3600\ s/h.$$

In this equation, habDriftConc is a habitat cell variable (Section III.G.1), and captureArea is calculated using a reactive distance approach.

We use the approach and parameter values of Van Winkle and others (1996) to identify a "reactive distance" at which 90 percent of prey items are captured *(table 15)*. This equation and its parameters werederived from data reported by Hill and Grossman (1993) relating velocity to capture success of rainbow trout:

$$reactDistance = fishLength \times$$

$$\frac{ln\left(\frac{0.9}{1-0.9}\right) - fishReactParamA - fishReactParamB\left(\frac{velocity}{fishLength}\right) - \left(fishReactParamC \times temperature\right)}{fishReactParamD}$$

Table 15—*Parameter values for drift feeding reactive distance.*

Parameter	Definition	Units	Value
fishReactParamA	Reactive distance constant	none	-5.91
fishReactParamB	Reactive distance velocity parameter	none	0.847
fishReactParamC	Reactive distance temperature parameter	1/C°	-0.0473
fishReactParamD	Reactive distance fish length parameter	none	1.74
fishTurbidMin	Turbidity below which reactive distance is unaffected	NTU	5.0
fishTurbidParamA	Multiplier in equation for turbidity effect on reactive distance	NTU^{-1}	-0.0227
fishTurbidParamB	Constant in equation for turbidity effect on reactive distance	none	1.12

At high velocities (e.g., 50 cm/s for fish 5 cm long; 155 cm/s for 15 cm fish), this equation produces negative values for reactDistance. We set such values to zero.

This formulation has the advantage of being developed from the data of Hill and Grossman (1993), who used a wide range of fish lengths (5-12 cm) and velocities (between 0 and 40 cm/s) for rainbow trout, which are relatively similar to the cutthroat trout we are modeling; it also produces very reasonable results (Section IX.C.6). The temperature dependence was determined from data collected at 5 and 15°C, approximately the range observed in Little Jones Creek. However, the approach has several potential limitations. Data were collected at reactive distances only up to 2.5 times the fish length were tested, whereas the model predicts reactive distances of more than four times the fish length. Because the data of Hill and Grossman (1993) were collected using only one size of prey (chironomids, which are small), the model may underestimate the distance over which fish capture larger prey. The model of Hughes and Dill (1990) has been used in several other models (Gowan 1995), but it has the disadvantage of having parameter values available only for arctic grayling; cutthroat trout may have significantly different swimming ability than grayling.

Turbidity effects on reactive distance are simulated using the simple model developed by Barrett and others (1992) for 9-19 cm rainbow trout. Barrett and others (1992) found a somewhat noisy but highly significant linear effect of turbidity (NTUs) on reactive distance as a fraction of reactive distance in clear water. This relationship is implemented in the model as follows:

- If *turbidity ≤ fishTurbidMin(NTU)*, then reactDistance is unaffected.
- If *turbidity × fishTurbidMin (NTU)*, then:

reactDistance = reactDistance × [(turbidity × fishTurbidParamA)
+ fishTurbidParamB]

- If the resulting value of reactDistance is less than zero, then it is set to zero. The parameter values from Barrett and others (1992; *table 15*) cause reactDistance to reach zero at a turbidity of 49 NTUs.

We define the width of the rectangular capture area as twice the reactive distance; this implements the assumption that fish are able to capture all drift that comes within the reactive distance to their left and right (as they face into the current). We compared the width of the capture area calculated by our drift-feeding method to the diameter of territories estimated by the field observations assembled

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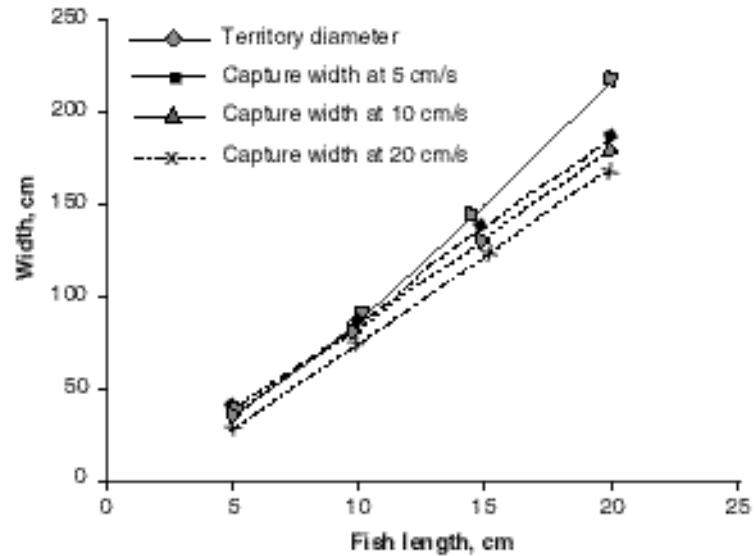
by Grant and Kramer (1990), assuming negligible turbidity. The capture area varies with velocity as well as fish size (hence the three lines for velocities of 10, 20, and 40 cm/s), but in general our model and the territory model of Grant and Kramer (1990) are very similar in how much stream width they allocate per fish, especially in the range of fish lengths (5-12 cm) used by Hill and Grossman (1993) to evaluate their parameters *(fig. 5)*. Gowan (1995) independently developed a similar capture area approach.

We define the height of the capture area to be the minimum of the reactive distance and the depth, as we assume fish are more likely to be near the stream bottom than at mid-depth when feeding. Our testing of this formulation indicates that the reactive distance is typically 3-5 body lengths in velocities of less than 50 cm/s. Especially in shallow habitat and for large fish, the depth will be less than reactive distance. Thus, we must limit the height of the capture area by the depth:

$$captureArea = [2 \times reactDistance] \times [min(reactDistance, depth)]$$

Increasing velocities increase the rate at which prey items are carried past a fish but decrease the reactive distance. As a consequence, the value of driftIntake peaks at intermediate velocities and reaches zero at high velocities (see the graphs in Section IX.C.6).

Active Searching Strategy—Actively searching for benthic or drop-in food is an alternative to the drift-feeding strategy. We simulate the food intake from this active searching strategy simply as:

$$searchIntake = habBenthicProd \times fishSearchArea \times$$

$$\times \frac{maxSwimSpeed - velocity}{maxSwimSpeed}$$

The value of searchIntake is set to zero if this equation produces a negative value. This equation assumes food intake rate for searching fish (searchIntake, g/h) varies linearly with the rate at which search food becomes available to fish (habSearchProd, g wet weight/h-cm^2; Section III.G.1). 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, however, may not be a contiguous piece of stream area: a small fish searching a small area closely may obtain the same food intake as a big fish spot-searching over a much larger area. Because fishSearchArea would be very difficult to measure, it is a good parameter to use for calibration. Because we do not make searchIntake a function of fish size, except for the effect of size on maxSwimSpeed, active searching is more likely to be the desirable strategy for smaller fish.

This equation also includes a term causing searchIntake to decrease linearly with the habitat cell's mean velocity and reach zero when velocity equals the fish's maximum sustainable swim speed (maxSwimSpeed). The equation for maxSwimSpeed is presented in the formulation for high velocity mortality (Section IX.D.2). This term is included to decrease the ability of a fish to see and search for food as velocity increases. (It does not represent the energetic cost of swimming at high velocities, which is considered in the respiration formulation in Section IX.C.3.) For habitat velocities above a fish's maximum swimming speed, searchIntake is zero.

Our estimation of habSearchProd and other growth parameters is discussed in Section IX.C.6.

Maximum Consumption—As part of the net energy intake calculations, we check to make sure calculated intake does not exceed the physiological maximum daily intake (Cmax, g/d). Field bioenergetics studies (Preall and Ringler 1989, Railsback and Rose 1999) indicate that actual food intake does not approach Cmax under typical conditions. However, Cmax serves the purpose of restricting intake and growth during low temperatures, a function otherwise lacking in the model (except that the time spent feeding becomes zero at temperatures below a threshold; Section IX.C.1). Cunjak and others (1998) cite evidence that low food assimilation efficiencies and gut evacuation rates, which can be represented by Cmax, limit energy intake in cold temperature.

There are a number of published equations for Cmax that include an allometric function, relating Cmax to fish size; and a temperature function. We use the equation:

$$Cmax\left(\frac{g}{d}\right) = fishCmaxParamA \times \left[fishWeight(g)\right]^{(1+fishCmaxParamB)} \times cmaxTempFunction$$

with the allometric parameters developed by Rand and others (1993) for rainbow trout *(table 16)*.

For the Cmax temperature function, our experience with lab studies indicates that only a simple approach is appropriate because Cmax is poorly defined and highly variable with fish condition, activity, food type, etc. (Myrick 1998, PG&E 1997). We use a simplified temperature function *(table 17)*, interpolating values between the points estimated from laboratory studies on rainbow trout (Myrick 1998).

Table 16—*Parameter values for allometric function of maximum consumption.*

Parameter	Definition	Units	Value
fishCmaxParamA	Allometric constant in maximum intake equation	none	0.628
fishCmaxParamB	Allometric exponent in maximum intake equation	none	-0.3

Table 17—*Parameter values for temperature function of maximum consumption.*

Parameter Name	Temperature (°C)	Parameter Name	maxTempFunction, cutthroat trout
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	0.0
fishCmaxTempT7	100	fishCmaxTempF7	0.0

Daily Food Availability—In determining the daily food intake rate for fish, our feeding formulation uses the total amount of drift (driftDailyCellTotal, g/d) and search (searchDailyCellTotal, g/d) food available each day in each cell. These daily food availability values are a function of the fish's feeding time because we cannot count food produced during non-feeding hours as available to the fish. We obtain the daily food availability rates from the hourly food availability rates described in Section III.G.2.

$$driftDailyCellTotal\ (g/d) = driftHourlyCellTotal\ (g/h) \times feedTime(h/d)$$

$$searchDailyCellTotal\ (g/d) = searchHourlyCellTotal\ (g/h)$$
$$\times feedTime\ (h/d)$$

IX.C.3. Respiration Costs and Use of Velocity Shelters

Conventional bioenergetics modeling approaches for fish (Hanson and others 1997) model respiration as the energetic cost of metabolism and swimming. We adopt this approach, modeling standard respiration that is independent of the fish's activity and an additional activity respiration that increases with the daily swimming speed.

Swim Speeds—We assume drift-feeding fish swim at a speed equal to their habitat cell's water velocity unless they have access to velocity shelter. Fish using the active search feeding strategy are assumed to swim at a speed equal to their cell's mean water velocity.

If a drift-feeding fish has access to velocity shelter, then we assume its swimming respiration is a fraction of its habitat cell's mean water velocity, determined by the input parameter fishShelterSpeedFrac. A number of studies have shown that "focal" water velocities (the velocity measured as closely as possible to the location of a fish assumed to have been drift-feeding) are related to, but less than, the mean column velocity at the same location. For example, we plotted focal versus mean column velocity for rainbow trout using data from Baltz and Moyle (1984), Baltz and others (1987), and Moyle and Baltz (1985). The focal velocity is consistently about 77 percent of the mean column velocity for observations made at the microhabitat scale *(fig. 6)*.

Unfortunately, we are unaware of any studies that relate focal velocity to mean water velocities at scales approximating habitat cells in the model. In the absence of a reliable way to estimate the daily swimming speed of a trout using velocity shelter, we assume a value of 0.3 for the parameter fishShelterSpeedFrac. We also use this formulation and parameter in the high velocity mortality function (Section IX.D.2).
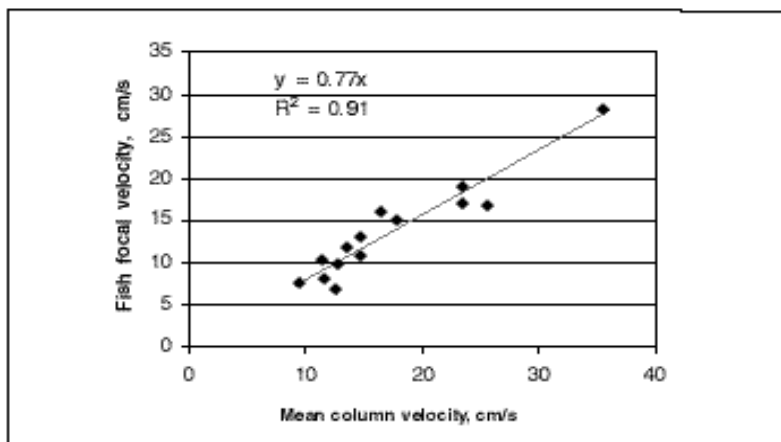
Velocity Shelter Access—We use the following steps to determine whether each fish has access to shelter in a habitat cell:

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

- 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 only if the sum of shelter areas occupied by more-dominant fish in a cell is less than the cell's total shelter area.

We assume each fish uses 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. With our approach, fish will share velocity shelters in high densities if our movement rules indicate it is favorable for them to do so.

Respiration Cost Model—We adopt the Wisconsin Model equation 1 for respiration (Hanson and others 1997), as modified by Van Winkle and others (1996), to apply the activity respiration rate only during active feeding hours (feedTime). We use the parameters that Rand and others (1993) developed for steelhead trout (converted from calories to joules; *table 18*). This formulation breaks respiration into two parts: standard respiration takes place 24 h/d and assumes no activity; activity respiration is the energy needed to swim during feeding. Total respiration is the sum of these two. Respiration costs are in j/d. The equations are:

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

and

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

where swimSpeed is the fish's swimming speed (cm/s) during feeding.

Table 18—*Parameter values for respiration.*

Parameter	Definition	Units	Value
fishRespParamA	Allometric constant in standard respiration equation	[1](j/d) $\times$ g$^{-0.78}$	30.0
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
fishShelterSpeedFrac	Swim speed reduction for fish using velocity shelter	none	0.3

[1]Empirical parameter with units that depend on fishRespParamB.

The standard respiration formulation above overestimates the effect of temperature on respiration rates and does not account for an observed decrease in respiration at temperatures above 22° (Myrick 1998). These problems cannot be fixed by changing parameter values, because of the Wisconsin Model equation's exponential temperature function. However, we have been able to make realistic calibrations of growth with this function. The decrease in respiration by inactive fish at high temperatures observed by Myrick (1998) in laboratory respiration chambers may not be applicable in many natural settings.

IX.C.4. Other Energy Losses

Most fish bioenergetic formulations include terms for energy losses due to egestion, excretion, and specific dynamic action. We do not include these terms because their effects are small compared to the large uncertainties in food availability and in the bioenergetics formulation and parameter values. These terms may be important at extremely low or high temperatures when the ability to digest food can limit growth, but we use the Cmax function to limit food consumption at extreme temperatures.

IX.C.5. Feeding Strategy Selection, Net Energy Benefits, and Growth

The feeding strategy selection, net energy, and growth methods calculate a fish's daily growth for a specific habitat cell, using the variables described in previous sections. Total food intake is calculated and total losses subtracted, determining whether drift feeding or active searching is more profitable. Competition among fish for food is implemented in these rules and our movement approach, which causes each fish's potential food intake in a cell to be limited by the food consumption of more dominant fish in that cell.

"Food" variables are in grams of prey; "Energy" variables are in joules. Prey energy density is used to convert grams of prey eaten to joules of energy; we adopt the value of Van Winkle and others (1996) for habPreyEnergyDensity of 2500 j/g. The change in fish weight (g/d) is equal to the net energy intake (j/d) divided by the energy density of a fish ("fishEnergyDensity," j/g). We use the energy density of Van Winkle and others (1996), 5900 j/g.

The following steps are used:

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

dailyPotentialDriftFood (g/d) = driftIntake (g/hr) × feedTime (h/d).

2. Determine how much drift intake is really available after more dominant fish have consumed their intake: this "dailyAvailableDriftFood" is equal to driftDailyCellTotal minus the drift intake of all drift-feeding fish already in the cell (Section III.G.2).

3. Calculate the actual drift intake, considering actual food availability and the physiological maximum intake, Cmax:

$$dailyDriftFoodIntake = \text{minimum of } (dailyPotentialDriftFood,$$
$$dailyAvailableDriftFood, Cmax).$$

4. Convert daily drift intake in grams of food to joules of energy:

$$dailyDriftEnergyIntake \ (j/d) = dailyDriftFoodIntake$$
$$\times habPreyEnergyDensity \ (j/g).$$

5. Use the bioenergetics equation to get net energy intake for drift feeding, with activity respiration dependent on whether the fish has velocity shelter:

$$dailyDriftNetEnergy \ (j/d) = dailyDriftEnergyIntake$$
$$- respStandard - respActivity.$$

6. Determine the daily active searching intake that would be obtained in the absence of more dominant fish in the cell; "dailyPotentialSearchFood" is determined from the hourly intake rates and hours spent feeding:

$$dailyPotentialSearchFood \ (g/d) = searchIntake \ (g/hr)$$
$$\times feedTime \ (h/d).$$

7. Determine how much search intake is really available after more dominant fish have consumed their intake: this "dailyAvailableSearchFood" is equal to searchDailyCellTotal minus the search intake of all search-feeding fish already in the cell (Section III.G.2).

8. Calculate the actual search intake:

$$dailySearchFoodIntake = \text{minimum of } (dailyPotentialSearchFood,$$
$$dailyAvailableSearchFood, Cmax).$$

9. Convert daily search intake in grams of food to joules of energy:

$$dailySearchEnergyIntake \ (j/d) = dailySearchFoodIntake$$
$$\times habPreyEnergyDensity \ (j/g).$$

10. Conduct the bioenergetics energy balance to get net energy intake for search feeding (no search-feeding fish have velocity shelter):

$$dailySearchNetEnergy(j/d) = dailySearchEnergyIntake$$
$$- respStandard - respActivity.$$

11. Select the most profitable feeding strategy:

bestNetEnergy (j/d) = maximum of *(dailyDriftNetEnergy,*
dailySearchNetEnergy).

12. Convert net energy intake to grams of growth:

dailyGrowth (g/d) = bestNetEnergy / fishEnergyDensity (j/g).

IX.C.6. Feeding and Growth Calibration

Because many variables affect growth, it must be calibrated incrementally so that reasonable results are likely before trying to calibrate growth in the full model, where flow and movement are additional major factors affecting growth. We started the calibration process by estimating initial parameter values for the food intake and growth formulation after coding it in a spreadsheet. Parameter estimation concentrated on adjusting the search and drift food availability parameters so that feeding strategies and growth rates met criteria that we developed from field observations of habitat use and laboratory growth data. For this process, we ignored depletion of food by competing fish.

We used the following criteria for initial estimates of food intake and growth parameters:

- Daily food intake should be in the range of 20 to 50 percent of Cmax. Cmax should rarely if ever limit food intake. This criterion is based on field research in which food intake was estimated from observed growth and bioenergetics models (Preall and Ringler 1989, Railsback and Rose 1999). (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, or when benthic prey are extremely abundant. 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 and others 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 (Myrick 1998, Myrick and Cech 1996). These lab growth rates are in the range of 2 to 6 percent of body weight per day, varying with temperature.

We estimated habDriftConc by assuming that, under ideal conditions, a 15 cm trout can catch food at a rate equal to 50 percent of its Cmax. This assumption is based on field evidence that in summer, average trout get 30 to 35 percent of Cmax (Railsback and Rose 1999). Under assumed conditions of 15° C, 50 cm/s velocity (which provides maximum intake), and a mid-summer feeding time of 16 h/d, 50 percent of Cmax is 0.19 g of food per hour. Our drift feeding method provides this intake when the value of habDriftConc is 2×10^{-10} g/cm^3.

The value of habDriftRegenDist was estimated by assuming a cell that contains 15 cm trout, each 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. Further, we assume that the fish get an intake of 30 percent of Cmax, or 0.13 g/h, and that under these conditions drift food production equals consumption by the trout. To provide this level of drift food production, the value of habDriftRegenDist must be approximately 500 cm.

The assumptions used to estimate search intake parameters are a search-feeding fish consumes the production of 2 square meters so that the value of fishSearchArea is 20,000 cm²; and a 5 cm trout can maintain zero growth by search feeding for 16 h/d at 15° (an intake of 0.006 g/h). These conditions give a value of 3×10^{-7} g/cm²/h for habSearchProd.

These parameter estimates provide the food intake levels (evaluated as the fraction of Cmax) and growth (evaluated as percent of body weight per day) shown in *figures 7-8*. For comparison to these parameter estimates, we did not locate any published estimates of the rate at which food becomes available, or is eaten by trout, at the stream bottom; published estimates of invertebrate production do not separate drift from any invertebrates eaten at the benthic surface. The rate at which food drops in from overhead (part of our search food production) is also rarely measured. Poff and Huryn (1998) report overall food production rates (in Atlantic salmon streams) in the range of 4 to 24 g dry weight per m² per year, which converts to $10 - 60 \times 10^{-7}$ g/cm²/h (assuming a typical ratio of 20 for dry:wet weight; Hanson and others 1997). Our estimate of habSearchProd appears reasonable compared to this value: we would expect habSearchProd to be a relatively small but not negligible fraction of the total production rate.

We show food intake *(fig. 7)* and growth rates *(fig. 8)* for 5 and 15 cm trout, as a function of cell velocity. For these graphs, the temperature was 15°, depth was 50 cm, and feeding time was 16 h/d. Food intake is reported as the percent of Cmax, growth as percent body weight per day.
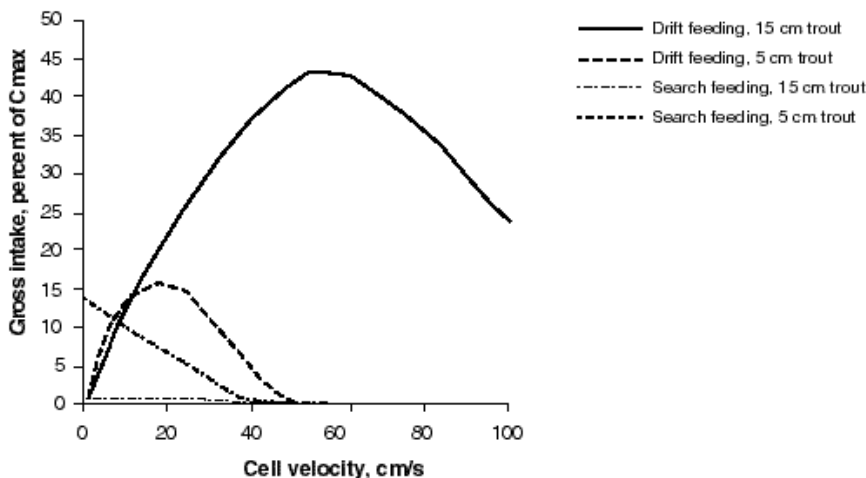
Figure 7 —Variation in gross food intake with velocity for two sizes of trout, using drift or search feeding.
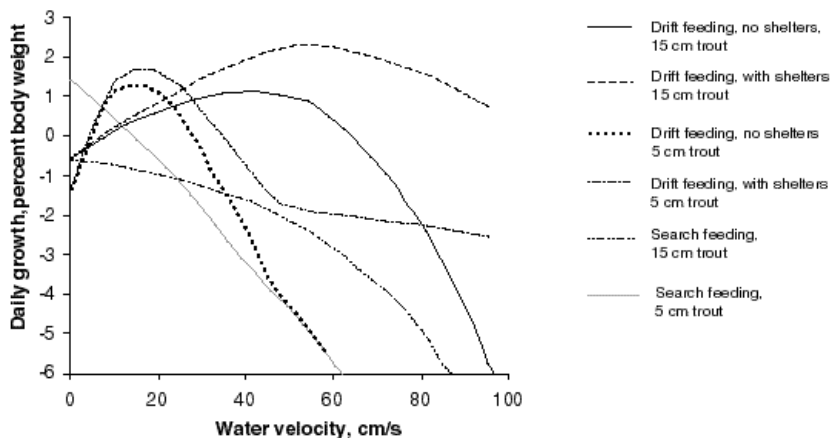
Figure 8 —Variation in growth rate with velocity for two sizes of trout, drift and search feeding strategies.

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

- 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.

- Search feeding is a profitable strategy only for small fish in low velocities.

- The relative benefits of drift feeding increase with fish size.

- Larger fish can drift feed profitably over a wider range of velocities, and at higher velocities, than can smaller fish.

Calibration of the full model (Section VII.A) resulted in relatively minor changes in value for the parameters habDriftConc (1.5×10^{-10} g/cm^3 instead of the preliminary estimate of 2×10^{-10}) and habSearchProd (7×10^{-7} g/cm^2/h instead of the preliminary estimate of 3×10^{-7}).

IX.D. Fish Survival Probabilities

The survival probability methods determine the daily probability of a fish surviving individual mortality sources, typically as a function of habitat and fish size and condition. These methods are used for two purposes: they are used in the movement destination rules to evaluate each potential destination site (Section IV.B.2), and in survival simulations to determine if and how each fish dies each day (Section IV.D). We use the same survival probabilities for each of these purposes, assuming that fish are completely aware of actual mortality risks.

We do not provide a calibration parameter for any risks except the two predation risk functions. A calibration parameter lets the user adjust the magnitude of the risk without changing how it is related to fish and habitat variables. To reduce the number of processes adjusted in calibration, we assume that survival probabilities for high temperature, high velocity, stranding, spawning, and poor condition are less uncertain than predation and should not be used for calibration.

Users should be aware that seemingly high survival probabilities can result in low survival over time. For example, a 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.

The survival probability formulations make extensive use of logistic functions, which are useful for depicting how many survival factors vary between 0 and 1 in a nonlinear way. We define these logistic curves by using parameters that specify the point at which the logistic function equals 0.1 and 0.9. (These lower and upper logistic curve dependent variable values of 0.1 and 0.9 are set via the fish parameters LOWER_LOGISTIC_DEPENDENT and UPPER_LOGISTIC_DEPENDENT.)

We simulate seven mortality sources. Parameter estimation and calibration of survival is discussed at Section IX.D.8.

IX.D.1. High Temperature

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

Table 19—*Parameter values for high temperature mortality.*

Parameter	Definition	Units	Value
mortFishHiTT9	Daily mean temperature at which high temperature survival is 90 pct	°C	25.8
mortFishHiTT1	Daily mean temperature at which high temperature survival is 10 pct	°C	30.0
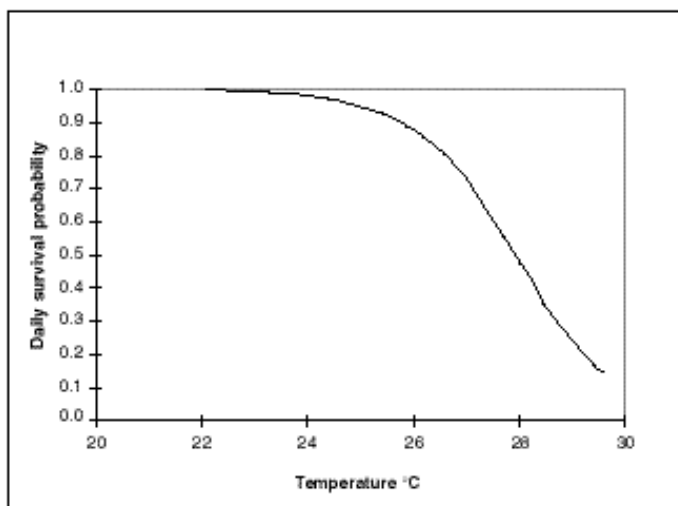
Figure 9 —Survival probability function for high temperatures.

Although input to the model includes only daily mean temperature, mortality is related to the daily maximum as well as the mean (although the relative importance of mean vs. maximum temperature is not clear; Dickerson and Vinyard 1999, Hokanson and others 1977). The survival probability function therefore includes an assumed difference between mean and peak temperatures. The temperature mortality parameters could be re-evaluated for sites with particularly high or low diurnal temperature variations.

Because high temperature mortality is poorly known and variable (especially in relation to daily mean temperatures), we use a decreasing logistic equation defined by the temperatures where this survival probability is equal to 0.9 and 0.1. Lethal temperatures appear similar among trout species (Behnke 1992). Recent laboratory data showed approximately 60 percent survival of golden trout (*O. 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 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°. Considering this literature and the low diurnal variation in temperature at our study sites, we fit parameters to provide survival of 0.98 at 24°, 0.88 at 26°, and < 0.5 at 28° (*fig. 9*; *table 19*). Lethal temperatures have not been observed at the Little Jones study sites.

IX.D.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 we expect it to kill fish often, but because it is a significant factor affecting fitness. Mortality caused by high velocities is not observed in nature because fish avoid them via movement. However, we must include this risk to cause such movement to occur in the model. Velocities posing

mortality risk are widespread at high flows. Our feeding model (Section IX.C.6) predicts that growth rates become negative at water velocities just below the onset of high velocity risk.

The survival probability is based on the ratio of the swimming speed required to remain in a cell to a fish's maximum sustainable swim speed, a function of fish size. Larger fish are better able to resist higher velocities than smaller fish are. We determine a fish's swimming speed the same way we do for calculating respiration energy costs (Section IX.C.3). 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 fishShelterSpeedFrac.

First, we estimate the fish's maximum sustainable swim speed (maxSwimSpeed). As used in our model with its daily time step, this variable should be a speed that fish can swim for hours, not a burst or short-term maximum speed. Myrick (1998) measured "critical swimming speed," a high estimate of sustainable speed; Myrick cites references indicating that trout may start to use white (fast-twitch) muscle fibers at 90 to 95 percent of the standard critical swimming speed. A better estimate of the speed fish can sustain for long periods is 90 percent of the critical speed (Myrick, personal communication). Myrick (1998) measured critical swim speed at temperatures between 10 and 19°C for four strains of *O. mykiss.*; he also cites other studies in which critical swimming speed has been measured for *O. mykiss* and cutthroat trout at similar temperatures. These measurements are subject to a number of potential errors, including that laboratory fish may not be in good exercise condition. These data show a lack of temperature dependence and good correspondence among studies *(fig. 10)*.

Griffiths and Alderdice (1972) made extensive measurements of swimming speed over temperatures between 2 and 26°C for juvenile coho salmon. These were the basis of the swimming speed model of Stewart (1980), which was also adopted in the individual-based model of Van Winkle and others (1996). These measurements showed gradual increase in sustainable swimming speed as temperature increased from 2 to about 20°, approximately doubling over this range. Swimming performance dropped off sharply at temperatures above about 20°. However, the data presented by Griffiths and Alderdice (1972) do not allow the effect of fish length to be separated from temperature effects. It seems reasonable to conclude from all the evidence that temperature has a relatively small effect on sustainable swimming speed except at temperatures approaching a fish's physiological tolerance limits. The model used by Van Winkle and others (1996) estimates swim speeds well above the critical swim speed measurements.

Figure 10 —Observed critical swim speeds.

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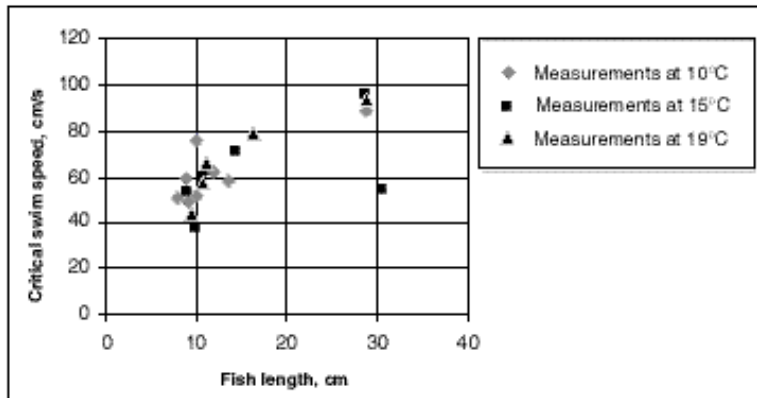
We use a maximum sustainable swim speed equation that is a simple linear function of fish length:

$$maxSwimSpeed = [fishSwimParamA \times fishLength]$$

$$+ fishSwimParamB.$$

It assumes sustainable swim speeds are 0.9 times the measured critical swim speeds, using linear regression on the data in *figure 10* (excluding the outlier at fish length of 30.8 cm and critical speed of 54 cm/s). The predicted sustainable swim speeds for trout of 4, 10, and 30 cm length are 40, 51, and 88 cm/s.

A decreasing logistic function relates survival probability to the habitat cell velocity divided by the fish's maximum swim speed *(fig. 11)*. The parameters for this function *(table 20)* are chosen so that high velocity mortality is negligible at cell velocities less than maxSwimSpeed, reflecting that the laboratory apparatus for measuring swim speeds does not have the kinds of turbulence and fine-scale velocity breaks that trout can use to swim at speeds less than the cell mean and that stream fish are likely to be in better condition than laboratory fish.

Table 20—*Parameter values for high velocity mortality.*

Parameter	Definition	Units	Value
fishSwimParamA	Length coefficient in maximum swim speed equation	1/s	1.83
fishSwimParamB	Constant in maximum swim speed equation	cm/s	33.00
mortFishVelocityV9	Ratio of mean column velocity to maximum swim speed at which high velocity survival is 90 pct	none	1.4
mortFishVelocityV1	Ratio of mean column velocity to aximum swim speed at which high velocity survival is 10 pct	none	1.8
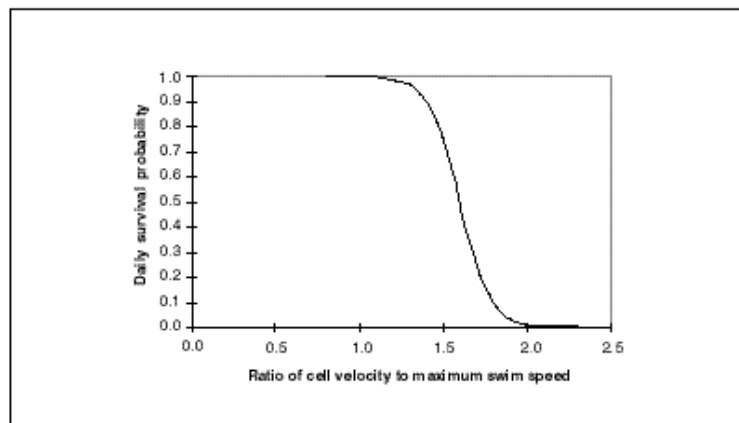
Figure 11 —Survival probability function for high velocity.

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IX.D.3. Stranding

We include a stranding survival probability factor to represent mortality of fish that are unable to move away from very low depths as flows decrease. Our movement rules provide a very strong incentive for fish to move from a cell that has zero depth, but there may be cases where a fish is limited by its maximum movement distance from reaching a cell with non-zero depth or no better habitat is available for other reasons. Our formulation was not designed for evaluation of stranding mortality from rapidly varying flows, as our time step of 1 day is too large.

Our formulation makes survival of stranding an increasing logistic function of depth divided by fish length *(fig. 12; table 21)*. Because our terrestrial predation function does not represent the greatly increased likelihood of predation mortality when depth is extremely low (Harvey and Stewart 1991), we include this risk as part of stranding mortality. The stranding survival function does not distinguish whether fish in very low or zero depths die from the lack of water or by predation.

Our 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 average 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.

IX.D.4. Spawning

We adopt the approach of Van Winkle and others (1996) for modeling spawning mortality. On the day a female fish spawns, its spawning survival is equal to the input parameter mortFishSpawn. Otherwise, spawning survival is 1.0.

Figure 12 —Survival probability function for stranding.
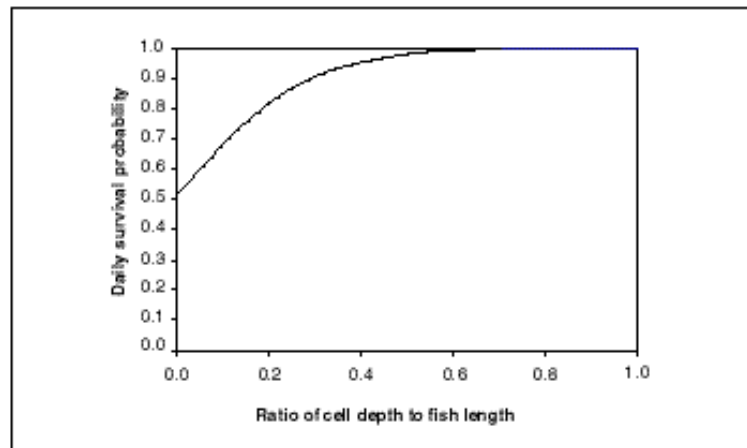
Table 21—*Parameter values for stranding mortality.*

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

We found few data that address mortFishSpawn. Stearley (1992) states that survival of spawning for *anadromous* populations of cutthroat trout is 40 to 50 percent, higher than the 5 to 40 percent survival estimated for steelhead. In the absence of spawning survival estimates for resident cutthroat trout, we use a value of 0.9.

This approach only inflicts spawning mortality on females, since we do not keep track of which males spawn (Section IV.A). Therefore, caution should be applied if spawning mortality is used to calibrate the abundance of large adults. (If there is evidence that spawning mortality in males is important to model accuracy, it could be simulated by identifying a large male near the spawning site and imposing mortality on it.)

IX.D.5. Poor Condition

Fish in poor condition (low weight in relation to length) probably suffer higher mortality risks from starvation, disease, and predators. (We assume the separate predation mortality applies to healthy fish.)

We use an increasing logistic function to represent survival probability as a function of condition *(fig. 13; table 22)*. Parameters were selected to reflect that disease can occur (though is less likely) when condition is relatively good and our non-standard definition of condition factor (Section IV.C) that has a maximum of 1.0. These parameters result in a 4 percent probability of surviving for 30 days when condition is 0.6, a 50 percent probability when condition is 0.7, and 96 percent probability when condition is 0.9.

In evaluating the condition-based survival parameters, it must be taken into consideration that these are daily survival probabilities and low condition factors are likely to persist for a number of days. Even apparently high survival values (e.g., 0.90) will result in a low chance of survival until weight can be regained.
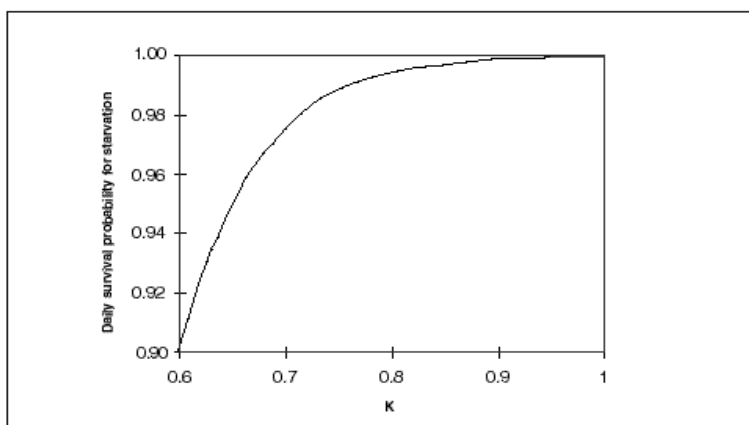
Figure 13 —Survival probability function for poor condition.

Table 22—*Parameter values for poor condition mortality.*

Parameter	Definition	Units	Value
mortFishConditionK1	Fish condition factor at which survival is 10 pct	none	0.3
mortFishConditionK9	Fish condition factor at which survival is 90 pct	none	0.6

IX.D.6. Terrestrial Predation

Terrestrial predators are birds and mammals. Our formulation is designed to represent predation by a mix of such predators as otters, raccoons, snakes, herons, mergansers, kingfishers, and dippers. Characteristics of terrestrial predators affecting the survival probability function include that they are generally bigger than the trout, poorer swimmers than adult trout, 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, risks are year-round, and the ability to detect prey from the air is important to predator success.

Our formulation assumes a minimum survival probability that applies when fish are most vulnerable to terrestrial predation and a number of "survival increase factors" that can increase the probability of survival above this minimum. We model survival increase factors as functions with values between zero and one, with higher values for greater protection from predation. Because we assume the survival increase factors act independently, we obtain the terrestrial predation survival by increasing the minimum survival (decreasing the difference between minimum survival and 1.0) by the maximum of the independent survival increase factors. This assumption is expressed mathematically as:

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

Using the maximum survival increase factor has several important numerical advantages over the alternative of multiplying all the survival increase factors together to adjust the overall predation risk. If we used the alternative of multiplying all the survival increase factors together, then the value of terrPredSurv could be several orders of magnitude less than the value of mortFishTerrPredMin, the input and calibration parameter; and the magnitude of terrPredSurv could be overly sensitive to small changes in a fish's condition. These characteristics would make results difficult to understand and calibrate. Also, multiplying the survival increase factors together would make the value of terrPredSurv a function of the number of survival increase factors as well as the value of these factors; as a result, adding or removing a survival increase factor could significantly alter fish abundance and require re-calibration of predation survival. By using our approach, survival increase factors can be added or removed, and they will not make order-of-magnitude changes in the overall predation survival rate.

The value of mortFishTerrPredMin is assumed to be the daily probability of surviving terrestrial predation under conditions where the survival increase factors are minimal (offering no reduction in risk). Because field data for estimating this minimum survival are unlikely to be available, we recommend estimating it by calibrating the model to observed abundance and habitat use patterns. The magnitude of this mortality source can vary with site conditions: e.g., rivers that have open, exposed banks are expected to have higher terrestrial predation rates. Before calibration, we assumed a value of 0.95 for mortFishTerrPredMin. Calibration of the full model (Section VII.A) resulted in a value of 0.99.

Our model parameter values for terrestrial predation mortality include seven survival increase factors *(table 23)*. These factors may vary among sites. Additional factors may be needed in some situations. (The effect of any factor can be turned off by setting its parameters to yield a constant value of zero.)

Depth—Fish are more vulnerable to terrestrial predators when in shallow water (Harvey and Stewart 1991) likely because they are easier for predators to locate and catch. We model the depth survival increase factor as an increasing

Table 23—*Parameter values for terrestrial predation mortality.*

Parameter	Definition	Units	Value
mortFishTerrPredMin	Daily survival probability due to terrestrial predators under most vulnerable conditions (calibration constant)	none	0.99 (calibration value)
mortFishTerrPredD1	Depth at which survival is 10 pct of maximum	cm	5
mortFishTerrPredD9	Depth at which survival is 90 pct of maximum	cm	100
mortFishTerrPredL9	Fish length at which survival is 90 pct of maximum	cm	3
mortFishTerrPredL1	Fish length at which survival is 10 pct of maximum	cm	6
mortFishTerrPredF9	Feeding time with survival 90 pct of maximum	h	0
mortFishTerrPredF1	Feeding time at which survival is 10 pct of maximum	h	18
mortFishTerrPredV1	Velocity at which survival is 10 pct of maximum	cm/s	20
mortFishTerrPredV9	Velocity at which survival is 90 pct of maximum	cm/s	100
mortFishTerrPredH9	Distance to hiding cover at which survival is 90 pct of maximum	cm	-100
mortFishTerrPredH1	Distance to hiding cover at which survival is 10 pct of maximum	cm	500
mortFishTerrPredT1	Turbidity with survival 10 pct of maximum	NTU	10
mortFishTerrPredT9	Turbidity with survival 90 pct of maximum	NTU	50
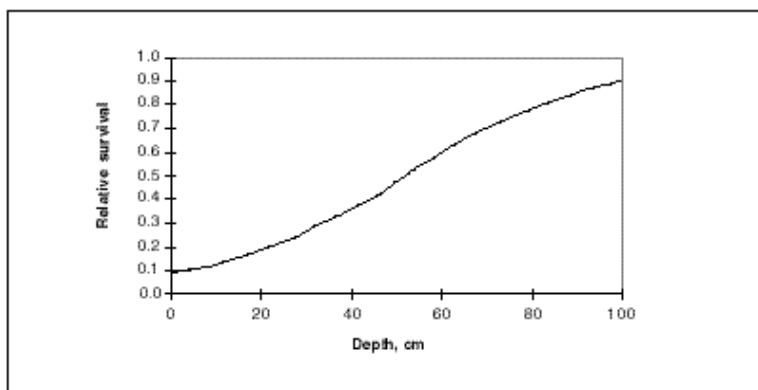
Figure 14 —Depth function for terrestrial predation mortality.

logistic function: survival increases as depth increases *(fig. 14)*. Power (1987) indicates that predation by birds is low at depths above 20 cm, although predators that are larger or better swimmers (herons, mergansers, otters) are likely effective at greater depths. (The very high risk of terrestrial predation that occurs when fish are in near-zero depths is included in stranding mortality; Section IX.D.3.)

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 factor. We located no direct literature directly relating terrestrial predation to turbidity. Instead, we consider the observed effect of turbidity on the ability of fish to detect prey (Barrett and others 1992, Vogel and Beauchamp 1999; Section IX.C.2), which shows the ability to detect drifting invertebrates unaffected at turbidities of 5 NTUs but declining to zero at 50 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. We therefore assume that turbidity has little effect at values below 5 NTUs but reduces terrestrial predation risk almost completely at 50 NTUs *(fig. 15)*.

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. However, because dippers (*Cinclus mexicanus*) prey on trout fry and other small fish (Thut 1970), very small fish are not invulnerable to terrestrial predation. We model decreasing survival of risk from terrestrial predators with fish length as a decreasing logistic function, with fish less than 4 cm in length being relatively protected *(fig. 16)*.

Figure 15 —Turbidity function for terrestrial predation mortality.
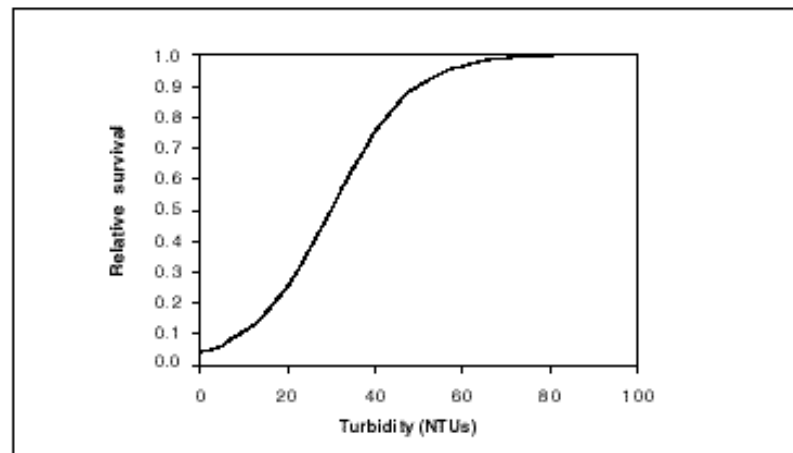
Figure 16 —Fish length function for terrestrial predation mortality.
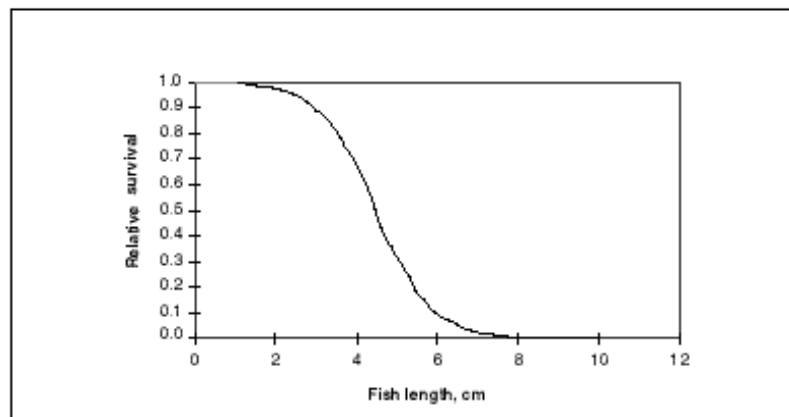
Feeding Time—Fish are assumed more vulnerable to predation when they are actively feeding instead of resting and hiding. (This factor is not designed to reflect how predation pressure changes diurnally; we assume terrestrial predators are present during both the day and night.) However, we assume a low level of predation can occur when fish are not feeding. We model the survival increase factor as a decreasing function of "feedTime" (h), a variable also used in calculating energy intake (Section IX.C.1). Parameters are chosen so that survival decreases nearly linearly with feedTime *(fig. 17)*.

Velocity—We include a function that increases terrestrial predation survival as water velocity increases. This function is based on the assumption that predators are less able to see and capture fish in turbulent water.

We model the survival increase factor as an increasing logistic function that provides nearly complete protection from terrestrial predators at velocities above 100 cm/s *(fig. 18)*.

Temperature—We do not include a temperature-based survival increase factor because there are no clear mechanisms that would cause predation pressure to change with temperature. At our study sites, ice cover does not provide protection from predation in winter. There is not a good basis for assuming predator activity is lower in winter; most of the predators we represent are warm-blooded and do not hibernate. In fact, such predators need additional food to maintain their metabolic needs in winter.
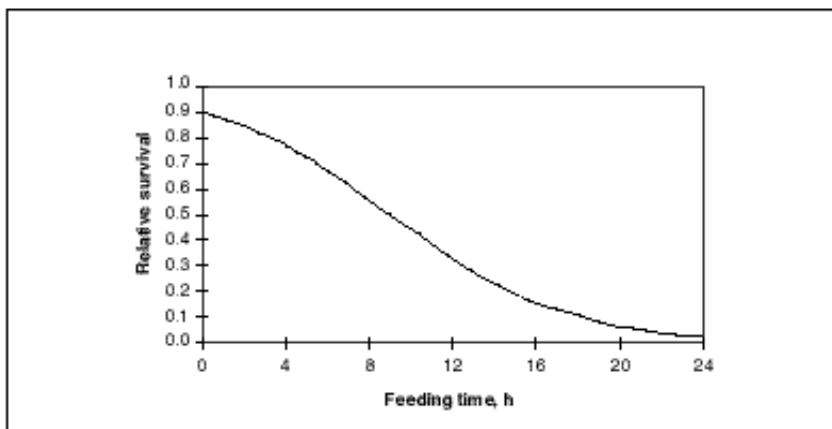
Figure 17 —Feeding time function for terrestrial predation mortality.
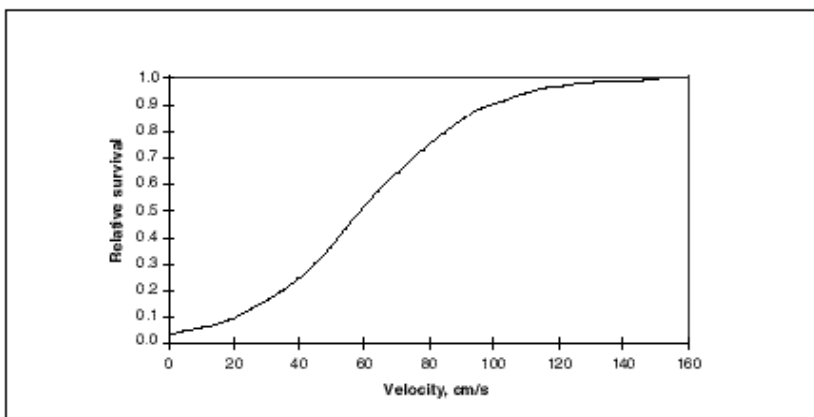
Figure 18 —Velocity function for terrestrial predation mortality.

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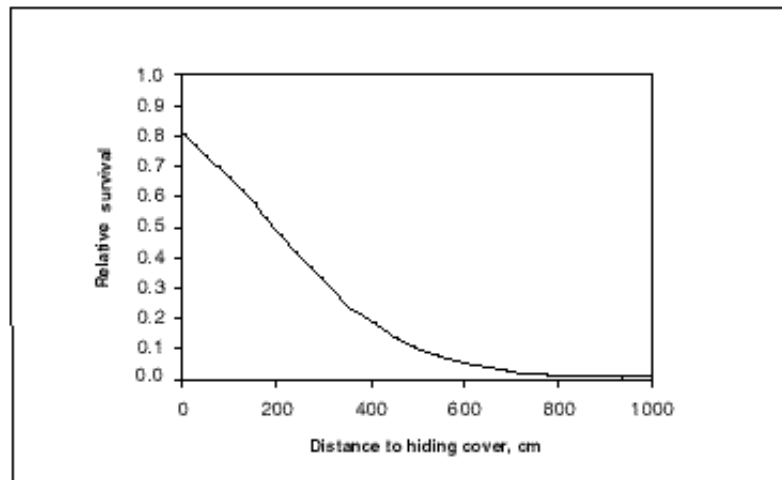
Distance to Hiding Cover—Fish can avoid mortality by hiding when predators are detected. The success of this tactic depends on the presence of hiding cover and the distance the fish must travel to reach it. The value of hiding cover is one habitat function that clearly occurs at a spatial scale different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

We model a distance-to-hiding survival increase factor using field estimates of the distance from the center of the cell to hiding cover for adult fish (Section VIII.H). This increase factor reflects the importance of nearby cover; at the Little Jones study sites there is sufficient cover so that all fish can hide within 10-20 m. We assume that very short distances to cover (< 1 m) 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, we model distance-to-hiding survival increase as a decreasing logistic function of the habitat input variable for distance to hiding cover *(fig. 19)*.

IX.D.7. Aquatic Predation

Our aquatic predation formulation assumes that this risk results from adult trout, the only predator fish in our Little Jones Creek sites. Therefore, only juvenile trout are vulnerable to aquatic predation. We simulate the effect of adult trout density on aquatic predation risks, making this survival probability the only one with direct density dependence.

The risk of predation by adult trout is generally highest for small fish in deeper water (Power 1987). As with terrestrial predation, we assume a minimum survival probability that applies when fish are most vulnerable to aquatic predation, and define a number of survival increase factors:

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

The value of mortFishAqPredMin (unitless) is assumed to be the daily probability of surviving aquatic predation under conditions where the survival increase factors offer no reduction in risk. As with terrestrial predation, because

data for directly estimating aquatic risks are unlikely to be available, we recommend estimating mortFishAqPredMin by calibrating the model to observed abundance and patterns of habitat selection by juvenile fish.

Diet data from the Little Jones Creek sites indicate that cannibalism by cutthroat trout occurs at a low rate: fewer than 1 percent of adult fish contained juveniles. However, even this low rate results in a significant mortality risk: 10 adults catching fish on 1 percent of days results in 37 mortalities per year. The risk of predation also appears to be an important factor driving habitat selection (Brown and Moyle 1991): avoiding predation is likely a key reason why small fish prefer shallow water. In this section, we use a preliminary value of 0.95 for mortFishAqPredMin (Section IX.D.8). Calibration of the full model (Section VII.A) resulted in a value of 0.997.

We do not include a factor for distance to hiding cover in computation of the risk from aquatic predators, as we do for risk from terrestrial predators (Section IX.D.6). This decision was made because only small trout are vulnerable to aquatic predators, and we assume small trout are capable of hiding almost anywhere in the complex substrate of our study sites.

We include a survival increase factor for turbidity that is based on the experimental observations and citations provided by Gregory and Levings (1999). 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). One mechanism that can offset this reduced encounter rate is that turbidity also reduces the vulnerability of adult trout to terrestrial predation, making them more likely to forage in shallow habitat where small fish are likely to be found (Section IX.D.6; Vogel and Beauchamp 1999).

Our aquatic predation survival formulation includes six survival increase factors, and several parameter values were used (table 24).

Table 24—Parameter values for aquatic predation mortality.

| Parameter	Definition	Units	Value
mortFishAqPredMin	Daily survival probability due to aquatic predators under most vulnerable conditions (calibration constant)	none	0.997 (calibration value)
mortFishAqPredP9	Predator density at which survival is 90 pct of maximum	cm^{-1}	0.0005
mortFishAqPredP1	Predator density at which survival is 10 pct of maximum	cm^{-1}	0.004
mortFishAqPredD9	Depth at which survival is 90 pct of maximum	cm	10
mortFishAqPredD1	Depth at which survival is 10 pct of maximum	cm	20
mortFishAqPredL1	Fish length with survival 10 pct of maximum	cm	4
mortFishAqPredL9	Fish length with survival 90 pct of maximum	cm	8
mortFishAqPredF9	Feeding time with survival 90 pct of maximum	h	0
mortFishAqPredF1	Feeding time with survival 10 pct of maximum	h	18
mortFishAqPredT9	Temperature with survival 90 pct of maximum	°C	2
mortFishAqPredT1	Temperature with survival 10 pct of maximum	°C	6
mortFishAqPredU9	Turbidity at which survival is 90 pct of maximum	NTU	80
mortFishAqPredU1	Turbidity at which survival is 10 pct of maximum	NTU	5

Predator Density—The only aquatic predators in our Little Jones Creek sites are large trout. Considering observed predator–prey size ratios for salmonids (Amundsen and others 1995) and the size distribution of cutthroat trout in Little Jones Creek, we assume all trout ≥ age 2 are potential cannibals. (Compared to the alternative assumption of specifying a length at which trout become piscivorous, using age as the criterion makes the computer implementation easier and provides a buffer against effects of poorly calibrated growth rates.)

The trout model tracks the abundance of trout ≥ age 2, allowing us to simulate the effect of predator density on survival probability. Post and others (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 1,000 m³. This result supports a logistic-like relation between adult trout density and juvenile trout survival probability, but is not directly applicable because it was obtained in lakes where cover and other habitat complexities may mediate the effect of predator density, and because risks were evaluated over 1 hour periods, whereas our model uses a daily time step.

There are three options for representing the density of predators: the total number of piscivores in the model reach, the number of piscivores per unit stream area, and the number of piscivores per unit stream length. The first alternative would make the survival function parameters highly site-dependent because the probability of piscivorous fish encountering prey becomes a function of the length of the reach being modeled. It is not clear whether the second or third alternative best reflects the mechanisms of piscivory; if we assume prey are likely to be in the stream margin habitat (where they are typically observed), then the number of predators per length of stream may be the best representation. The second option requires the minor computational burden of calculating stream area as it varies daily with flow.

We model the survival increase factor for adult trout density using a decreasing logistic function of the number of age 2+ trout per cm of stream length *(fig. 20)*. (We use trout numbers per cm to maintain our units conventions; Section I.C.1.) Parameters were chosen to reflect near-zero risk when predator density is zero and a steep decline in survival as predator density exceeds one adult trout per 6 to 8 m of stream length. These parameters should be re-evaluated for new modeling sites, considering stream width and the extent of shallow habitat.

Figure 20 —Predator density function for aquatic predation mortality.
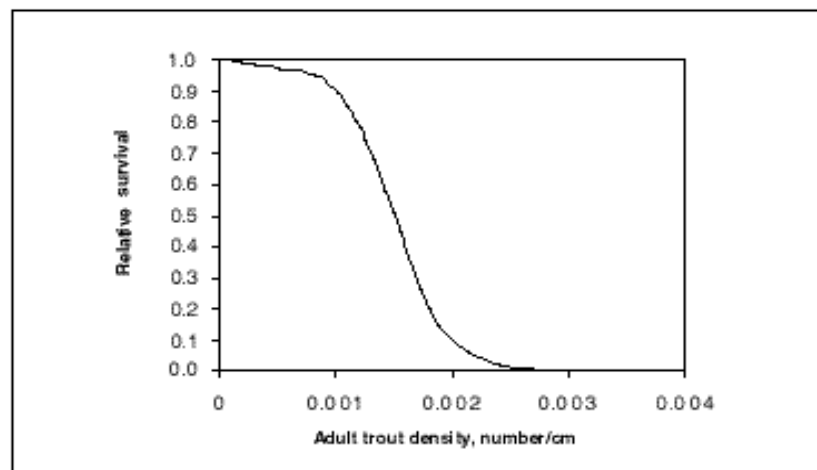
Model users should be aware that this survival increase factor eliminates aquatic predation risk if the model is run with no adult trout, and the absence of this risk can have a major effect on juvenile trout habitat selection. It should also be noted that the dependence of aquatic predation survival on the density of trout age 2 means this survival probability may decrease suddenly on January 1, when the age of all fish is incremented; Section I.C.4.

Depth—Aquatic predation is assumed to be low in water shallow enough to exclude large fish. We model the depth survival increase factor as a decreasing logistic function, with protection provided at depths less than 15 cm *(fig. 21)*.

Fish Length—Large fish are less vulnerable to aquatic predation because they can out-swim predators and because piscivorous cutthroat trout are unable to swallow large prey. The length survival increase factor is an increasing logistic function, with fish greater than 10 cm being very unlikely to be eaten by trout *(fig. 22)*. Our parameter values reflect the relatively small size of the predators at our study site. Models of sites with larger predators should reflect the corresponding vulnerability of larger trout.
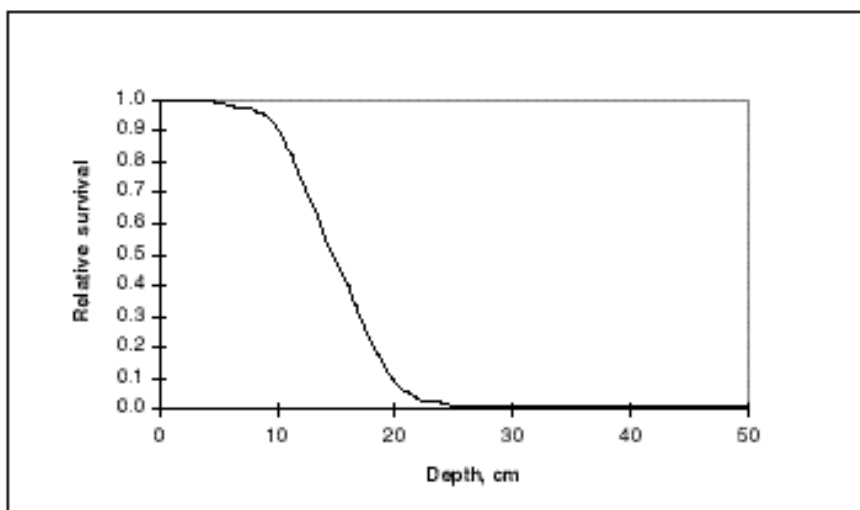
Figure 21 —Depth function for aquatic predation mortality.
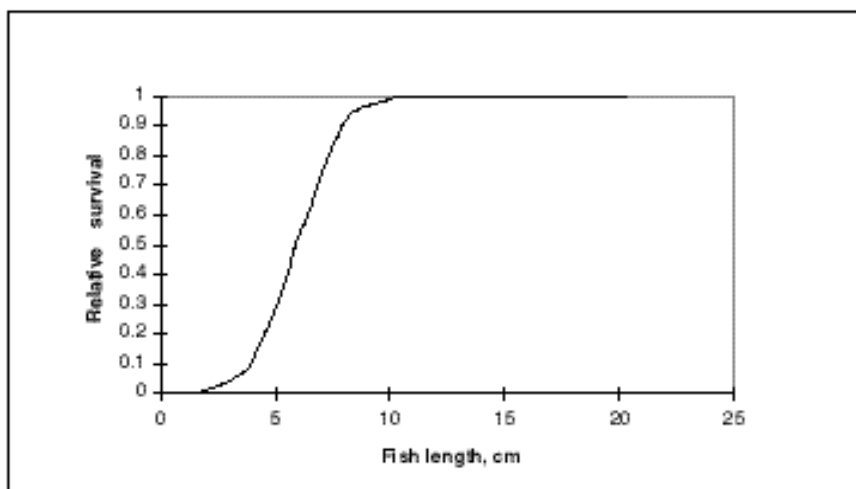
Figure 22 —Fish length function for aquatic predation mortality.

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Feeding Time—This survival increase factor is the same for aquatic predation as it is for terrestrial predation. The survival increase is a decreasing logistic function of "feedTime," the number of hours per day spent foraging.

Low Temperature—This survival increase factor reflects how low temperatures reduce the feeding activity of predatory fish and therefore reduce predation pressure. We base this factor on the bioenergetics of the trout predators, using a decreasing logistic function *(fig. 23)* that approximates the decline in maximum food consumption (Cmax) with declining temperature (Section IX.C.2).

We neglect the decline in aquatic predation risk that results from high temperatures; such a decline would result from predatory trout not feeding at extremely high temperatures.

Turbidity—The turbidity factor represents how encounter rates between predator and prey fish decline as turbidity increases. In an experiment using tethered juvenile salmonids, Gregory and Levings (1999) observed predation rates two to three times higher in turbid habitat (27 to 108 NTUs) than in habitat where turbidity was negligible. Predation was reduced by not eliminated in turbid habitat. We estimated parameters that provide no protection from aquatic predation at low turbidities and a 50 percent reduction in risk at 40 NTUs *(fig. 24)*. As turbidity continues to increase toward extreme values, aquatic predation risk continues to decrease but is not eliminated.

Figure 23 —Temperature function for aquatic predation mortality.
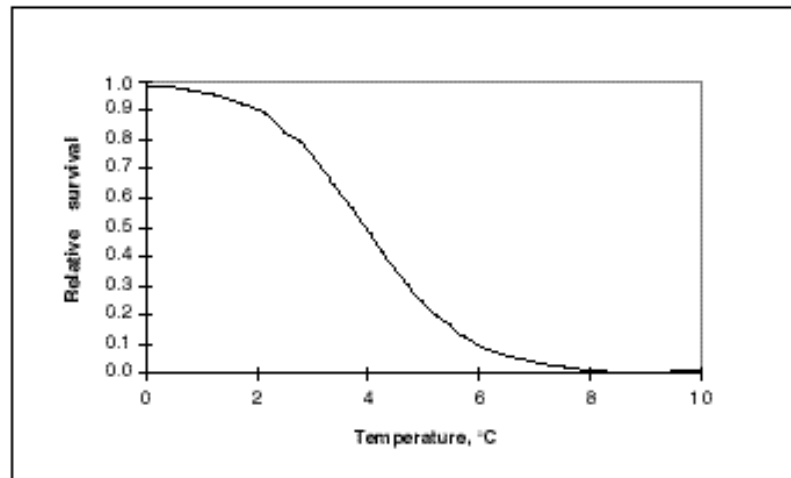
Figure 24 —Turbidity function for aquatic predation mortality.
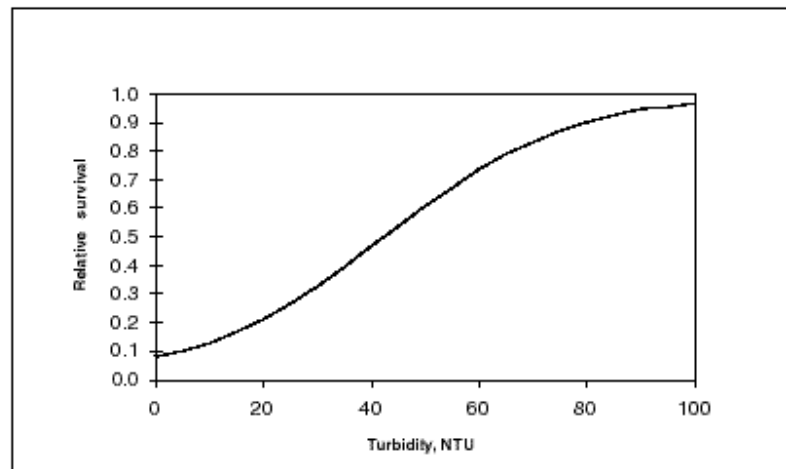
IX.D.8. Total Survival: Parameter Estimation and Effects of Fish Size, Depth, and Velocity

The total survival probability for a fish is calculated by multiplying together the probabilities of surviving separate mortality risks. *Figures 25-28* 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 0.95, and have the values for other parameters. Turbidity, distance to hiding cover, and adult trout density were assumed to have no effect on survival. The daily survival is shown on a scale of 0.8 to 1.0 because survival probabilities below 0.8 result in very high mortality over several days.

The 3 cm trout *(fig. 25)* are vulnerable mainly to aquatic predators, and the 10 *(fig. 27)* and 20 cm *(fig. 28)* trout are vulnerable mainly to terrestrial predators. The 5 cm trout *(fig. 26)* are vulnerable to both categories of predators.

Survival rates in the modeled trout populations are not only a function of the survival probability formulation and parameters but also of the feeding and growth formulation and food availability. 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. As a consequence, little parameter estimation can be conducted prior to calibration in the full model.

Our approach to parameter fitting and calibration is to assume most of the uncertainty in the survival formulation is in the two base predation parameters (mortFishTerrPredMin and mortFishAqPredMin) and use only these two for calibration, and define the following criteria for calibrating survival in the full model:

- When adult trout diet data are available, predicted aquatic predation mortality should match observed rates.
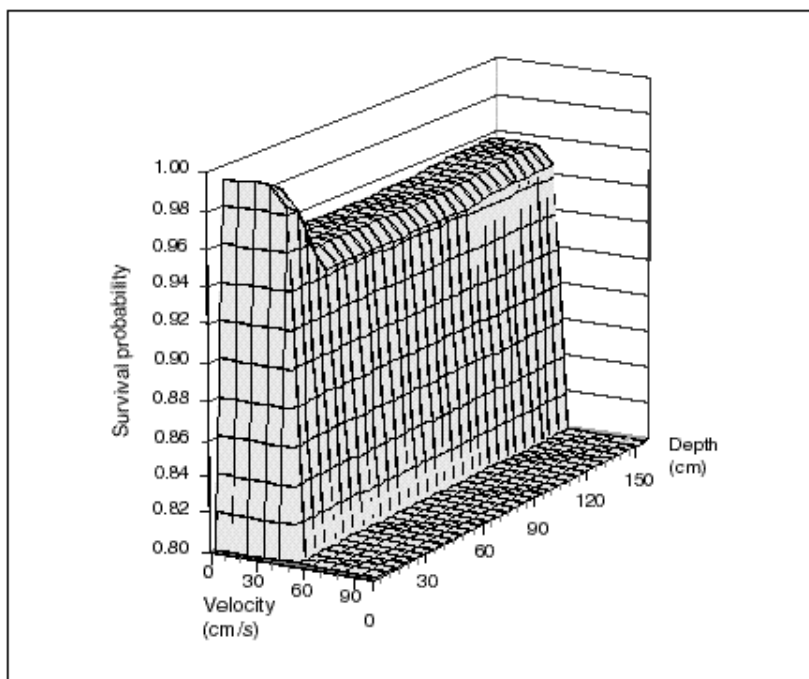

Figure 25 —Total survivial probablity as a funciton of depth and velocity, 3 cm trout.

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- The calibrated model should reproduce observed patterns of habitat use. Preferences for depth and velocity have been documented to vary with fish size, season, and competition.

- The formulation should produce age-specific survival rates that reproduce observed age distributions.

- The overall survival rate should be reasonably closed to observed survival rates. Calibration may be easier for time periods when habitat conditions are relatively stable.

Figure 26 —Total survival probablity as a function of depth and velocity, 5 cm trout.
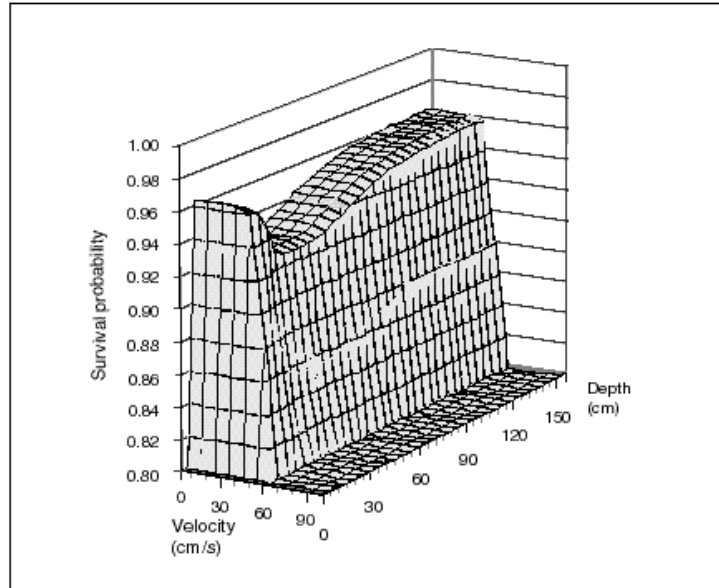
Figure 27 —Total survival probablity as a function of depth and velocity, 10 cm trout.
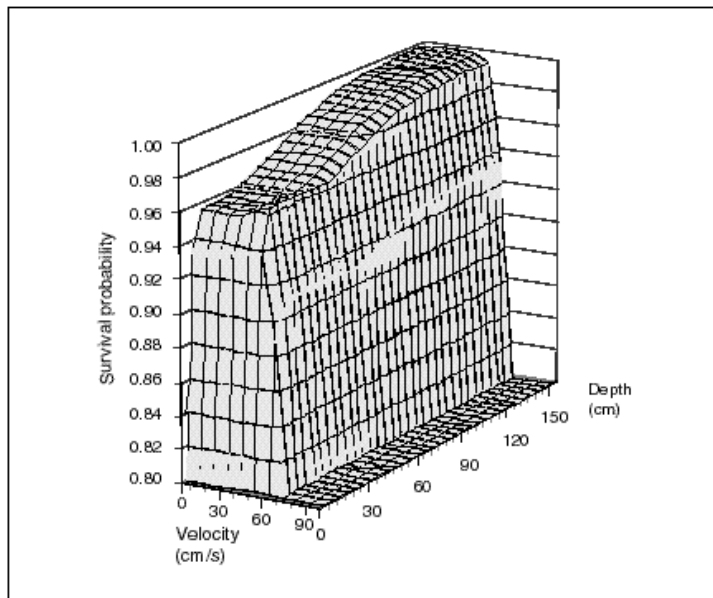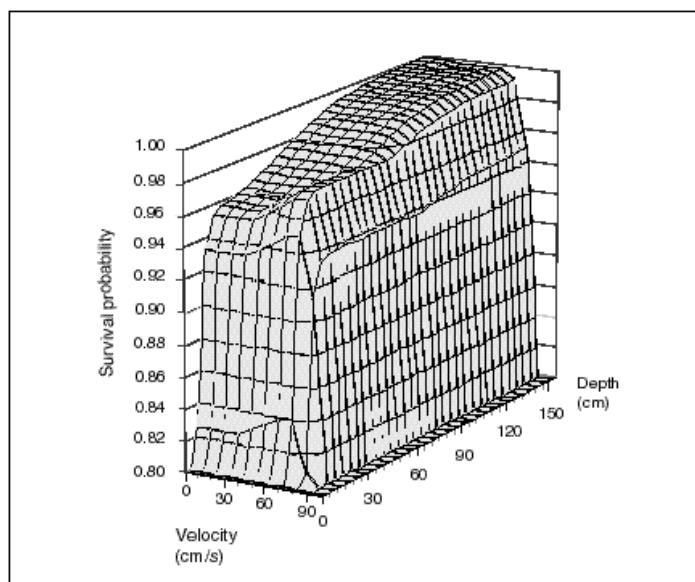
IX.E. Redd Survival Functions

The redd survival methods simulate each mortality source. For each such source, a survival function determines the daily fraction of eggs surviving (Section V.A). These fractions are each multiplied by the number of eggs remaining in a redd to calculate a new number of surviving eggs.

We do not currently have a redd survival function related to spawning gravel quality. Although spawning gravel quality has several effects on redd success (Kondolf 2000), we currently choose not to simulate these effects to avoid additional complexity and data requirements. Our spawning site selection criteria (Section IV.A.2) allow a fish to spawn in a cell that has little or no gravel; we inflict no redd mortality penalty for doing so. The exception is that if superimposition occurs in a cell with little spawning gravel (which seems unlikely unless gravel is very rare), then superimposition mortality is likely to be high. In Little Jones Creek, spawning gravel appears abundant.

IX.E.1. Dewatering

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 we do not distinguish between eggs and alevins, we do not model these processes mechanistically or in detail. We simply assume that, if depth is zero, then the daily fraction of eggs surviving is equal to the input parameter "mortReddDewaterSurv." We use a value of 0.9 for this parameter.

For study sites where dewatering of redds is an important management issue, this formulation could be expanded to model the effects of dewatering and low velocities on eggs and alevins in more detail.

IX.E.2. Scouring and Deposition

Scouring and deposition mortality results from high flows disturbing the gravel containing a redd. 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 alevins from emerging.

This redd mortality source can be very important to trout populations. There is a fitness benefit to spawning early: offspring emerge earlier and have a competitive advantage over young-of-year fish that emerge later. However, this benefit is to some extent offset by greater risk of redds being scoured in streams (including Little Jones Creek) where high flows occur in winter and spring.

There are methods for predicting the potential for scouring mechanistically as a function of shear stress and substrate particle size, but geologists now understand that scour and deposition at the scale of individual redds are highly stochastic processes. At least in gravel-bed streams like Little Jones Creek, it is virtually impossible to predict where scour and deposition will occur at various flows (Haschenburger 1999, Wilcock and others 1996). Consequently, we adapted 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.

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 shear stress. We assume 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 input parameter mortReddScourDepth (cm). Consequently, the probability of a redd not being destroyed (scourSurvival) is equal to the proportion of the stream scouring or filling to a depth less than the value of mortReddScourDepth. This scour survival probability is estimated from the exponential distribution model of Haschenburger (1999); the proportion of the stream scouring to less than a given depth is the integral of the exponential distribution between zero and the depth:

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

The value of scourParam is estimated by Haschenburger empirically:

$$scourParam = 0.33e^{-1.52 \times (shearStress/0.045)}$$

The value of shearStress (a dimensionless indicator of scour potential) is estimated as:

$$shearStress = \frac{\rho RS}{(\rho_s - \rho)D}$$

where is the density of water ($1 \ g/cm^3$); R is the reach-average hydraulic radius; S is the reach-scale energy slope; $_s$ is the density of sediment, approximated as $2.7 \ g/cm^3$; and D is the mean substrate particle diameter.

The model can calculate value of shearStress, as a function of flow rate, for the study site. This can be done by using the approximation that the hydraulic radius is equal to the average depth, which can be calculated each day as a function of flow, and by providing the slope as an input parameter. However, this method may introduce significant errors because it assumes that all the resistance to flow through the study site is a result of bed roughness (controlled by shear stress). In reality, the flow resistance in most river channels is partly due to "form roughness," the effect of channel bends and large obstacles in backing up the flow. Using the above equation to estimate shear stress for our model reaches, which have numerous sharp bends and obstacles, would overestimate shear stress and the potential for scouring.

We circumvented this potential problem by estimating a relation between shear stress and flow at a nearby stream reach that is relatively straight and obstacle–free and has low form roughness, with a slope and substrate diameter similar to the modeling reach. From this shear stress reference site, we obtained the following empirical relation between shear stress and flow (m^3/s):

$$shearStress = mortReddShearParamA \times flow^{\,mortReddShearParamB}$$

The distance down from the gravel surface to the top of a redd's egg pocket appears to be an appropriate measure of mortReddScourDepth. 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. Deposition is especially likely to reduce survival if it includes fine sediment. The literature suggests 10 cm is a reasonable value of mortReddScourDepth for small trout like Little Jones Creek cutthroat (DeVries 1997).

Our parameters *(table 25)* produce a decreasing relation between peak flow and survival of redd scouring *(fig. 29)*.

This model of scouring estimates the probability of a redd surviving scour in each high-flow event, not on a daily time step. The single survival probability is applied to all redds, assuming that if scouring occurs, then no eggs survive.

Table 25—*Parameter values for scour and fill redd mortality.*

Parameter	Definition	Units	Value[1]
mortReddShearParamA	Multiplier for the relation between flow and shear stress	s/m^3	0.019
mortReddShearParamB	Exponent for the relation between flow and shear stress	none	0.383
mortReddScourDepth	Depth of scour or fill assumed to destroy a redd	cm	10

[1] Values determined at a site on Little Jones Creek about midway between the upper and lower modeling reaches. These values probably poorly represent the small tributary modeling site.
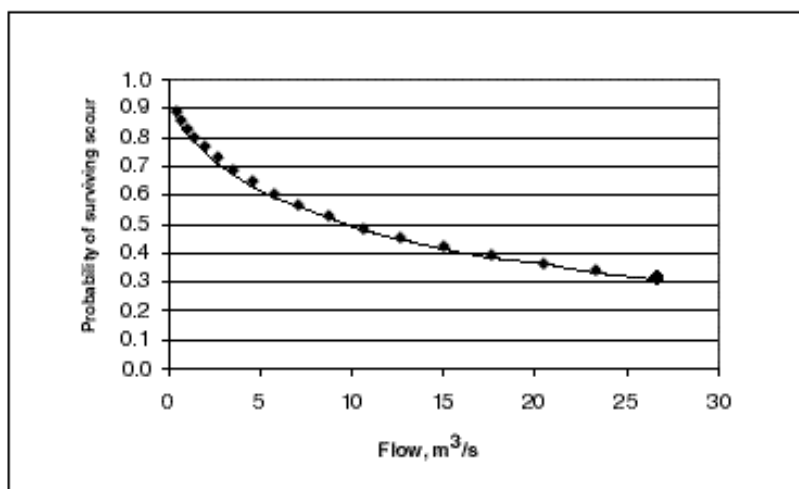

Figure 29 —Scour and fill redd survival function.

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Therefore, we apply this risk factor only once per cycle of rising then falling flows, using these steps:

- The redd scour survival probability is calculated only on days when the flow is greater than both the previous day's flow and the next day's flow; this means the flow peaked on the current day. When this peak occurs, the following two steps are followed; on all other days, the fraction of eggs surviving is 1.0.

- One value of scour survival probability (scourSurvival) is calculated for the whole model reach, using the above equations for the current flow. This probability is used for all redds.

- For each redd, a uniform random number between zero and one is drawn. If the value of this 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.

IX.E.3. Low Temperature

Both low and high temperatures cause mortality in eggs at temperatures much different than those causing mortality in fish. We model mortality caused by high and low temperatures separately and use logistic functions, which seem to represent the available data well. Because temperatures are moderate at the Little Jones Creek study site, both low and high temperature redd mortality are expected to be minor.

We assume the fraction of eggs surviving low temperatures per day is an increasing logistic function of temperature. We estimated parameter values from data compiled by Brown (1974), keeping in mind that because eggs incubate slowly at low temperatures, even apparently high daily survival rates can result in low egg survival over the incubation period.

The data compiled by Brown (1974) indicate that rainbow trout spawn at temperatures as low as 3 to 5°C and eggs have a 90 percent survival rate over a 100-d incubation period at 3°C (egg survival = 0.999). We also assumed a daily survival rate of 0.9 at 0°C and found logistics parameters that reproduce these two points *(fig. 30; table 26)*. We adopt these values for cutthroat trout.
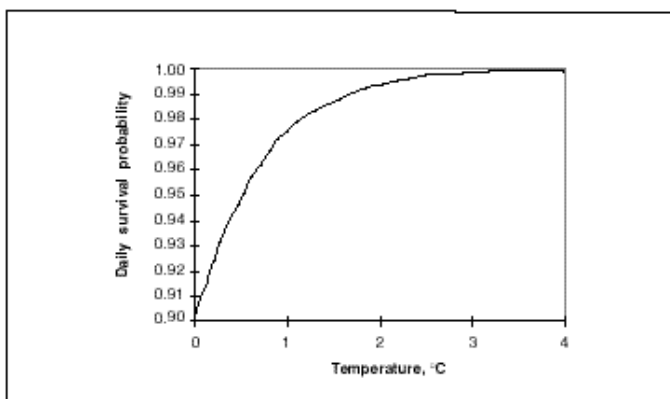
Figure 30 —Low temperature redd survival function.

Table 26—*Parameter values for low temperature redd mortality.*

Parameter	Definition	Units	Value
mortReddLoTT1	Temperature at which low temperature survival is 10 pct	°C	-3
mortReddLoTT9	Temperature at which low temperature survival is 90 pct	°C	0

IX.E.4. High Temperature

We assume the fraction of eggs dying from high temperatures per day is an increasing logistic function of temperature *(fig. 31)*. We adopt rainbow trout values that were 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°. Our parameters *(table 27)* appear to indicate high survival at high temperatures, but in fact cause low survival if temperatures are elevated for long periods.

IX.E.5. Superimposition

Superimposition 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. For simplicity, our formulation currently assumes that superimposition is a random occurrence, with spawners not intentionally spawning over existing redds. The study by Essington and others (1998) indicates that stream trout may indeed intentionally superimpose their redds over existing ones, a practice that has the advantages of reducing the work necessary to clean redd gravels and the competition that the spawner's offspring will face. Our formulation could easily be modified to study the complex effects that intentional superimposition might have.

We assume that, if another redd is laid in the same habitat cell, the risk of superimposition mortality is a function of the area disturbed in creating the new redd and the area of spawning gravel available. We simulate superimposition by:

1. Determining, for each redd on each day, if one or more new redds were created in the same cell.

2. If so, the risk of superimposition mortality occurring (reddSuperImpRisk, unitless daily probability) is equal to the area of a redd divided by the area of spawning gravel.
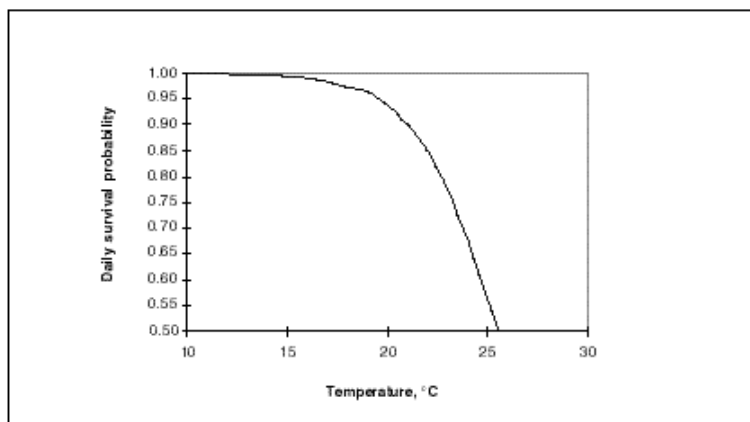

Figure 31 —High temperature redd survival function.

Table 27 —*Parameter values for high temperature redd mortality.*

Parameter	Definition	Units	Value
mortReddHiTT9	Temperature at which high temperature survival is 90 pct	°C	21
mortReddHiTT1	Temperature at which high temperature survival is 10 pct	°C	30

3. A random number (uniform distribution between zero and one) is drawn; if it is less than the value of reddSuperImpRisk, then superimposition mortality occurs.

4. If superimposition mortality occurs, then the fraction of eggs surviving is a uniform random number (0-1).

5. Steps 2-4 are repeated if more than one new redd was placed in the cell.

The value of reddSuperImpRisk can be greater than 1.0 if cellFracSpawn is very small. In the event that cellFracSpawn is zero, we assume there is no risk of superimposition because there is no gravel to be disturbed by another spawner.

Because of the way we use the parameter reddSize in this formulation, we define it to be the area that a spawner disturbs in creating a new redd. On the basis of field observations at Little Jones Creek, we assume reddSize to be 1200 cm^2 (the area of a circle with a diameter of 35 cm) for resident cutthroat trout.

X. Model Development Priorities and Research Topics

This section describes additional model development and research needs that we identified in designing this model formulation. The development and research needs include:

- Ways to address potentially important ecological processes that are currently absent, simplified, or poorly quantified in the current formulation; and

- Approaches that better match the modeling philosophy we attempt to follow (Section I.A).

Some of these model development ideas would add complexity and computational burden to the model but may also add key elements of realism. An experimental approach can be taken to adding them, determining their relative costs and benefits.

One general model development priority is to conduct an analysis of the sensitivity of model predictions to individual model components and parameters. A useful sensitivity analysis would focus on parameters and equations, which are not as well defined and supported by independent literature.

X.A. Imposed versus Emergent Behaviors

The trout model's formulation includes both methods that force fish to behave in ways that have been observed in real trout populations ("imposed behaviors") and those that let fish choose their behavior to maximize their fitness, producing "emergent behaviors." An example of imposed behavior in some models of stream salmonids is that fish are forced to maintain territories, although there are times when doing so is not beneficial or realistic. Our feeding formulation does not impose territorial behavior; instead, our feeding and movement rules let fish select habitat to maximize their long-term fitness. Habitat selection patterns emerge from the combination of habitat dynamics and fitness-seeking behavior, sometimes producing behavior similar to territoriality but sometimes not. This approach is more appealing from a theoretical sense because we model the underlying causes of behavior instead of imposing behaviors that may not always be appropriate.

We have found the "Unified Foraging Theory" and related approaches (Bull and others 1996, Mangel and Clark 1986, Thorpe and others 1998) for modeling decision-making to be especially valuable for individual-based modeling with emergent behaviors. In contrast to traditional foraging theory, these approaches make the critical and realistic assumption that fish base their decisions on the predicted mid- to long-term consequences.

X.A.1. Generalization of Movement Objectives

The model's rules for movement (habitat selection) allow fish to select the destination that maximizes a simple measure of their fitness ("expected reproductive maturity"; Section IV.B.2). These rules can be generalized to provide more accurate and complete measures of fitness for fish to maximize. Some changes may give fish more realistic habitat selection behaviors.

For instance, our movement rules let fish predict the effects of food intake on the risk of starvation and consider it in movement decisions. However, these rules currently do not consider the effect of predicted growth on other risks. For example, selecting a site that provides rapid growth would decrease a fish's risk of being eaten by another fish. Including the effects of growth on all risks would give fish a more accurate measure of the fitness benefits of alternative destinations.

The model's current fitness measure has only the simplest representation of how fish size affects reproductive success: a length threshold for spawning. Providing a more general representation of how fecundity and offspring survival depend on spawner size in the fitness measure appears to be a simple yet important way to make habitat selection and growth more realistic. This change would encourage adult fish to continue growing after attaining the minimum reproductive size.

X.A.2. Readiness to Spawn and Spawning Location

One example of imposed behavior in this model is our approach for determining the day when a fish spawns: we prohibit the fish from spawning except when a number of predetermined criteria are met, then use a stochastic rule to impose variation in the dates that fish spawn. Both the predetermined spawning criteria and the variation in spawning dates are imposed to make the behavior of model fish match that of real fish. Similarly, we use observed habitat preferences to determine where a fish should spawn.

A more mechanistic approach to these spawning decisions would be to model the fish's readiness to spawn (e.g., by tracking its energy reserves), and let each fish decide if, when, and where it spawns so that it maximizes the probability of producing fry that can compete well in the critical first summer of life. Simple models of how a fish predicts the effect of spawning location and timing on expected redd survival and fry viability could be developed from our existing redd development and survival formulation. An even more complete approach would incorporate the effects of spawning versus not spawning on reproductive value.

X.A.3. Allocation of Growth to Fish Length, Weight, and Gonads

The approach we adopt from Van Winkle and others (1996) for determining how much a fish grows in length when it gains weight unrealistically locks the fish into a predetermined length-weight relationship. It does not, for example, let fish store energy reserves that can be used later (Section IV.C). We also currently do not simulate the important energetic effects of gonad development and spawning.

A fitness optimization approach to allocation of growth seems feasible: let the fish allocate weight to length, muscle, fat, or gonads to maximize its expected fitness. This approach is similar to that tested successfully by Bull and others (1996). Such an approach could also contribute to a more mechanistic method for simulating readiness to spawn (Section X.A.1).

X.A.4. Diurnal Changes in Behavior and Hiding Cover Limitations

Fish vary their diel pattern of feeding and hiding (Heggenes and others 1999). If hiding is specifically modeled (it is not included in the current model), then the potential limiting effects of hiding cover can be simulated. The availability of winter hiding cover appears to be low and potentially limiting at

Little Jones Creek. Our current formulation is incapable of predicting seasonal (or habitat-related) changes in diurnal behavior; instead, we simulate only daytime feeding behavior (Section IX.C.1).

A potentially viable approach to incorporating concealment behavior may be to:

- Include the habitat cell's area of hiding cover in the habitat model and make survival during hiding a function of competition for hiding cover.

- Assume that hiding fish have no food intake and much lower mortality risk.

- Simulate how survival probabilities and food intake for feeding fish differ between day and night.

- Alter the model's movement rules so that they maximize expected reproductive maturity using a daily optimal combination of feeding versus hiding. A fish could choose to feed in the day and hide at night, hide in the day and feed at night, hide day and night, or feed day and night. This decision would incorporate the effect of the availability of hiding cover on survival probabilities when not feeding and perhaps differential feeding success at night versus during the day.

X.B. Habitat Model Issues

Despite the many years that stream trout habitat models have been used, frustrating limitations remain. The first three of these habitat-modeling issues are relevant to conventional habitat index models like PHABSIM (Railsback 1999).

X.B.1. Habitat Cell Sizes

The spatial scales used in models have crucial effects on results. Despite the popularity of habitat models for stream fish, we found a dearth of literature on how the ability to predict such fish characteristics as behavior, survival, and growth varies with spatial scale. Currently, we select the spatial resolution of our model (cell size) to approximate the scale at which microhabitat varies at the study site. The resolution we use seems reasonable, but research on what spatial scales are most appropriate for stream fish models with daily time steps would be welcome.

X.B.2. Accuracy of Hydraulic Simulations

We identified two problems with our hydraulic simulation approach that uses PHABSIM hydraulic models. One problem is that PHABSIM hydraulic models cannot simulate zero or very low velocities well, even in shallow margin habitats and especially in eddies and backwaters. This makes it difficult to model fish that prefer low velocities and shallow water, like age 0 trout. A second problem is that standard PHABSIM calibration methods tend to reduce the natural variation in depth and velocity in complex habitats. Because such variation makes model calibration difficult and results in unrealistic hydraulic predictions, model users tend to take the variation out during calibration (if they do not avoid it by biasing where hydraulic data are collected; Railsback 1999). Using more appropriate calibration measures can reduce this problem.

These two problems are largely due to the one-dimensional nature of the PHABSIM models and because they do not consider bedform roughness, even though bedform roughness often appears to be the most important process controlling stream velocities.

Two approaches for avoiding these problems are being considered by instream flow researchers. Two-dimensional finite-element hydraulic models can do a better job of representing margin habitat and can (in some cases) better accommodate spatial variation. These models can also have lower field data costs when modern surveying technologies are employed. Several research groups have looked at this class of models for instream flow studies but a model ready for routine use has not yet appeared.

The second alternative approach is using a statistical representation of habitat, treating field hydraulic measurements as point samples of a population instead of as a map of the stream environment (Dingman 1989). This approach has the disadvantages of being a less direct representation of the stream, not maintaining the spatial relations among habitats, and likely having burdensome requirements for collection of field data.

X.B.3. Variation in Velocity Shelter Availability

The drift-feeding component of our model indicates that velocity shelters are very important to trout energetics (Section IX.C.6). We currently assume that the area of a habitat cell with velocity shelters is constant (Section III.D). However, field observations indicate that the amount of velocity shelter varies with flow and is a function of fish size. For example, a small boulder may provide no velocity shelter during high flows, yet may provide abundant shelter for a juvenile fish during lower flows. Especially for sites where velocity shelters are limited, more realistic assumptions about velocity shelter may be valuable. However, modeling variation in shelter availability may introduce considerable computational burden and uncertainty.

X.B.4. Spatial and Temporal Variation in Food Availability

Food availability is a very important parameter that we currently simulate simply. Predictions of fish habitat use and population dynamics will be more accurate if we develop ways to simulate how food availability varies over space and time, and with habitat conditions (especially, with flow and temperature). One possibility is making the drift food regeneration parameter (Section III.G.1) a function of velocity, substrate type, or temperature. An example approach is the work of Morin and Dumont (1994) showing how aquatic insect production rates vary with temperature.

X.C. Fish Model Issues

X.C.1. Immigration and Emigration

Immigration and emigration of healthy fish are commonly observed phenomena, and we plan to incorporate these processes in future versions of the model. We especially will focus on movement of juvenile fish out of a small tributary into the creek's mainstem. We have not yet developed the methods for doing so. We will most likely develop approaches for simultaneously modeling a mainstem and tributary site and the movement of fish between them.

X.C.2. Movement Distances and Knowledge of Environment

We assume the distance over which a fish "knows" habitat conditions and considers potential movement destinations depends only on its length (Section IV.B.2). This approach seems simplistic. A more sophisticated approach to simulating how much habitat animals consider during movement decisions is to let each build its own map of the environment, with maps expanded via exploration. To maximize their predicted long-term fitness, animals can make random exploratory movements outside its known area that would improve its map of known habitat as an alternative to making fitness-maximizing movements within known areas. This approach has been used in the cowbird model of Harper and others (2000). A simpler but less mechanistic approach is to assume that the maximum distance over which fish can evaluate potential movement destinations varies randomly among individuals or over time.

X.C.3. Fitness Time Horizons for Movement

The fitness measure we use to evaluate movement destinations (Section IV.B.2) uses a fixed time horizon over which risks of starvation and other mortality sources are evaluated. There is little literature or evidence supporting

selection of a time horizon value. A similar modeling approach developed by Thorpe and others (1998) proposes time horizons reflecting a salmonid's activity or life history stages; for example, the fitness horizon for a trout overwintering in a cold climate could be the time remaining before active feeding can resume. It seems reasonable for the time horizon of adult trout to be the time remaining before the spawning season, over which the fish can build spawning energy reserves and produce gonads.

If the time horizon is variable, it could depend on the outcome of movement decisions: for example, the time horizon could be the time remaining before a fish achieves the length and weight needed for spawning. In this case, the time horizon would depend on net energy intake: cells providing higher growth reduce the time remaining before spawning size is achieved. The relative fitness offered by various habitat cells would depend not only on starvation and other risks but also on the time horizon resulting from the growth rate in the cell. There are a number of such research issues related to fixed or variable fitness time horizons.

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USDA Forest Service Gen. Tech. Rep. PSW-GTR-182. 2001.

XI.Input Parameter Index

XII. References

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