Simulation Analysis of Within-Day Flow Fluctuation Effects on Trout below Flaming Gorge Dam

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CONTENTS

CONTENTS (Cont.)

TABLES

TABLES (Cont.)

FIGURES

FIGURES (Cont.)

FIGURES (Cont.)

ACKNOWLEDGMENTS

NOTATION

The following is a list of the acronyms, initialisms, and abbreviations (including units of measure) used in this document.

ACRONYMS, INITIALISMS, AND ABBREVIATIONS

C_{max}	maximum grams of food consumed by a fish each day
ERM	expected reproductive maturity
GUI	graphical user interface
HSU	Humboldt State University
IBM	individual-based model
inSTREAM	individual-based Stream Trout Research and Environmental Assessment Model
inSTREAM-SD	*inSTREAM* with sub-daily time step
UDWR	Utah Division of Wildlife Resources
WSE	water surface elevation

UNITS OF MEASURE

ºC	degree(s) Centigrade	K	fraction of normal weight for a given length
cm	centimeter(s)		
cm^3	cubic centimeter(s)	kg	kilogram(s)
		km	kilometer(s)
d	day(s)		
		m	meter(s)
ft^3	cubic foot (feet)	m^2	square meter(s)
		m^3	cubic meter(s)
g	gram(s)	mL	milliliter(s)
h	hour(s)	NTU	Nephelometric Turbidity Unit(s)
j	joule(s)	s	second(s)

1 INTRODUCTION

1.1 PROBLEM STATEMENT

In addition to being renewable, hydropower has the advantage of allowing rapid load-following, in that the generation rate can easily be varied within a day to match the demand for power. However, the flow fluctuations that result from load-following can be controversial, in part because they may affect downstream fish populations. At Flaming Gorge Dam, located on the Green River in northeastern Utah, concern has been raised about whether flow fluctuations caused by the dam disrupt feeding at a tailwater trout fishery, as fish move in response to flow changes and as the flow changes alter the amount or timing of the invertebrate drift that trout feed on.

Western Area Power Administration (Western), which controls power production on sub-monthly time scales, has made several operational changes to address concerns about flow fluctuation effects on fisheries. These changes include reducing the number of daily flow peaks from two to one and operating within a restricted range of flows. These changes significantly reduce the value of the power produced at Flaming Gorge Dam and put higher load-following pressure on other power plants. Consequently, Western has great interest in understanding what benefits these restrictions provide to the fishery and whether adjusting the restrictions could provide a better tradeoff between power and non-power concerns.

Directly evaluating the effects of flow fluctuations on fish populations is unfortunately difficult. Effects are expected to be relatively small, so tightly controlled experiments with large sample sizes and long study durations would be needed to evaluate them. Such experiments would be extremely expensive and would be subject to the confounding effects of uncontrollable variations in factors such as runoff and weather.

Computer simulation using individual-based models (IBMs) is an alternative study approach for ecological problems that are not amenable to analysis using field studies alone. An IBM simulates how a population responds to environmental changes by representing how the population's individuals interact with their environment and each other. IBMs represent key characteristics of both individual organisms (trout, in this case) and the environment, thus allowing controlled simulation experiments to analyze the effects of changes in the key variables. For the flow fluctuation problem at Flaming Gorge Dam, the key environmental variables are flow rates and invertebrate drift concentrations, and the most important processes involve how trout adapt to changes (over space and time) in growth potential and mortality risk.

This report documents simulation analyses of flow fluctuation effects on trout populations. The analyses were conducted in a highly controlled fashion: an IBM was used to predict production (survival and growth) of trout populations under a variety of scenarios that differ only in the level or type of flow fluctuation.

1.2 STUDY OBJECTIVES

The objectives of the research reported here are to use an IBM and computer simulation experiments to analyze the following three specific problems:

1. How does the magnitude of within-day flow fluctuations affect production of trout in the Flaming Gorge Dam tailwater? Are higher peak flows (and, therefore, lower off-peak flows) more detrimental than lower peaks and higher off-peak flows?

2. What is the relative effect of "double peaking" (two load-following cycles per day) compared to single peaking on trout production? Are two cycles per day more detrimental than one?

3. How is trout production affected if flow fluctuations alter the timing or amount of invertebrate drift? In what ways could flow fluctuations affect the within-day pattern of drift, and how do such drift patterns affect trout production?

1.3 REPORT OVERVIEW

Section 2 describes the general methods used in this study and the major features of the trout IBM. A more complete description of the IBM is provided in the Appendix. Section 2 also describes the methods used in the simulation experiments to address the study objectives, especially the study sites and flow scenarios. Sections 3 to 5 separately describe each of the three simulation experiments used to address the three study objectives. These sections depict the experimental design, simulation results, and conclusions concerning each study objective.

Section 6 of this report provides a summary of the study and the overall conclusions drawn from the simulation experiments.

2 METHODS

2.1 ANALYSIS SCOPE

This section describes the overall scope and level of detail of the simulation analysis, to make it clear what it did and did not attempt to represent.

The analysis endpoint is trout production: the change in biomass (kilograms, kg) of the simulated population of trout within a study site over one year. The biomass added by stocking hatchery trout is represented in the simulations but not included as production. Even though the Flaming Gorge Dam trout fishery includes rainbow (*Oncorhynchus mykiss*), brown (*Salmo trutta*), and cutthroat trout (*Oncorhynchus clarki*), the simulation analysis treats all trout as a single species. This simplification was made because there are no known differences among trout species in model parameters that would strongly affect the results of this particular analysis.

The IBM does not represent movement of fish in or out of study sites, or migration of fish upstream and downstream in the tailwater area, which is undoubtedly an important process that could affect the distribution of trout among sites. Therefore, the simulation results should be viewed as an index of how conditions for trout production vary among scenarios at each site, not as predictions of how trout populations vary within or among sites.

The geographic scope of the analysis is from Flaming Gorge Dam downstream approximately 26 km to the Taylor Flat Bridge. This reach is represented by four study sites, which are described in Section 2.3.

Temporal variation in habitat conditions was represented by analyzing three types of years based upon the amount of spring runoff: dry, average, and wet. All experiments were based on simulations of one year.

2.2 SIMULATION MODEL

The analysis used the individual-based trout simulation model *inSTREAM-SD*, which is a member of the *inSTREAM* (individual-based Stream Trout Research and Environmental Assessment Model) family of river salmonid IBMs developed and maintained by Lang, Railsback & Associates and Humboldt State University (see www.humboldt.edu/~ecomodel). The *inSTREAM-SD* model was developed by modifying Version 2 of *inSTREAM* to represent sub-daily variation in flow (hence, the *SD* designation). Version 2 of *inSTREAM* is documented fully by Railsback and Harvey (2001; see also Railsback and Harvey 2002 and its digital appendix at www.esapubs.org/archive/ecol/E083/031/default.htm). Its modification as *inSTREAM-SD* is described in the appendix to this report, and was summarized by Railsback et al. (2005). Here, the characteristics of *inSTREAM-SD* most important to the simulation experiments are summarized.

2.2.1 Fundamental Assumptions

The *inSTREAM-SD* model was designed specifically to represent how river trout populations are affected by instream flow (from hourly changes up to seasonal and year-to-year variations) and temperature. Flow is assumed to affect depth and velocity, and depth and velocity are assumed to affect a trout's feeding and growth rates and mortality risks. Likewise, temperature is assumed to affect growth. Differences between day and night are explicitly represented. At night, trout are assumed to be less effective at capturing food, but also to have a lower predation mortality risk. Trout are assumed to adapt to the growth rates and mortality risks presented by their habitat in two ways. The first way is by choosing whether to feed or hide at each time step; hiding offers a much lower predation risk but no food intake, and therefore slightly negative growth. The second adaptive behavior involves choosing which habitat cell to occupy for either feeding or hiding; the value of a cell for feeding or hiding depends on its depth, velocity, hiding cover, and competition with larger trout for food and cover.

The model represents habitat as a two-dimensional reach of rectangular cells. Each reach represents a study site of several hundred meters in river length. Cells are typically 1 to 3 m in width (across the river) and up to 20 m in length.

Time is represented using time steps between one hour and a half-day in length. Flow input is hourly. To represent day and night and the effects of within-day flow changes, either of two events triggers the start of a new time step: (1) the change from night to day, or day to night; or (2) a change in hourly flow of 10% or more since the last time step. If flow does not vary during a day, then time steps start only at dawn and dusk. If flow does vary within a day, time steps also start at any hour at which flow has changed by at least 10%.

The inputs used to represent environmental factors that the model assumes are important include:

- *Hourly flow data*. Annual hydrographs of hourly flow values were developed to represent the full range of possible flow fluctuations within three different hydrologic year types.

- *Daily mean water temperature*. Temperature is a daily, not hourly, input because the equations and parameters used to model temperature effects on trout growth and survival are based on daily mean temperature.

- *Drift food concentration*. For most of the analyses, drift food concentration (grams of food per cubic centimeter of water) was assumed to vary daily as a function of water temperature. For the third study objective (Section 5), drift was represented as also varying hourly with flow.

- *Daily turbidity*. Turbidity (cloudiness of the water) decreases the ability of fish to capture food and makes the fish less vulnerable to predators. However, for these analyses, turbidity was assumed to be negligible because (1) there is very little information available, and (2) the Flaming Gorge Dam tailwater is

generally quite clear (except downstream of Red Creek when the creek's flow is high).

2.2.2 Trout Characteristics and Behaviors

The following discussion describes how *inSTREAM-SD* represents the ways that individual trout are affected by, and adapt to, their environment. This discussion does not include all of the processes in the model, but concentrates on those that are important below Flaming Gorge Dam.

2.2.2.1 Feeding and Growth

Feeding (the rate at which model trout capture food from the drift) is based on a number of field studies and previous models. Trout are assumed to maintain a feeding station and capture food as it drifts past. As velocity increases, the amount of food passing increases, but the distance over which fish can capture it successfully decreases. Consequently, food intake increases with velocity up to a peak, after which food intake decreases. Food intake increases linearly with the concentration of drift prey. However, food intake can also be limited by the rate at which a fish can process food; this rate is low at low temperatures.

Growth is modeled using standard bioenergetics equations (Hanson et al. 1997) calibrated for trout (Railsback and Rose 1999). This approach predicts a trout's growth as the difference between energy intake from food and energy losses due to metabolism. Metabolic losses increase with both temperature and swimming speed. If a fish uses a velocity shelter (waits for food behind cover such as a boulder), its swimming speed is reduced, so its growth is increased. Observations at Green River study sites indicated that velocity shelters are common, but tend to be partially embedded in sand, so they are not very effective. It was therefore assumed that velocity shelters reduce swimming speed by 50%.

One of the hypothesized effects of fluctuating flows that this study addresses is that feeding is disrupted when trout move in response to flow change. It was therefore necessary to represent this effect in the model. This was done by assuming a "feeding penalty time," which is a certain time period that a trout is assumed to swim at the cell mean velocity without feeding or hiding, if moving to a different cell. There are no field studies to support the choice of a value for the feeding penalty time, so a relatively conservative (likely overestimating the effect of movement on growth) value of 0.25 hour was used. An analysis of the effects of this assumption is included in Section 2.7.

2.2.2.2 Survival

The model represents a number of different kinds of mortality risk and how they vary with habitat. Of most interest in this study is the risk of predation by terrestrial animals; in particular, river otters (*Lontra canadensis*) and piscivorous birds (ospreys [*Pandion haliaetus*],

bald eagles [*Haliaeetus leucocephalus*], and common mergansers [*Mergus merganser*]) are commonly seen hunting in the study reach. Survival (the daily probability of not being killed) of terrestrial predation is modeled as a function of several habitat variables and trout behaviors:

- Survival is higher in habitat cells that are deeper and faster, conditions that make it harder for many predators to see and capture trout. However, these were assumed not to be strong effects in the Green River because (1) otters especially are strong swimmers and mergansers can dive and forage in relatively deep water, and (2) the river is so large that deep, fast cells are not necessarily turbulent or difficult to maneuver in.

- Survival is higher at night (risk is reduced by 70%). Otters sometimes feed at night, but bird predation is likely much lower.

- Survival is much higher (risk reduced by 99%) when trout are hiding in cover (e.g., boulders, vegetation, or woody debris that provide a visual screen from predators).

The probability of surviving starvation and disease (combined as "poor condition" mortality) is assumed to decrease as a fish's weight decreases during periods of negative growth. Trout are also assumed to be at risk of stranding, if they choose to occupy extremely shallow cells, and of exhaustion, if they occupy cells having velocities much higher than their sustainable swimming speed.

2.2.2.3 Behavior: Activity and Habitat Selection

The trout are modeled by assuming that they have two closely related adaptive behaviors: selecting which activity—feeding or hiding—to pursue and which habitat cell to occupy. These decisions are made each time step, so that model trout can adapt continually to changes in flow, temperature, competition with other trout, and their own condition. To make these decisions, a model trout first identifies the cells it potentially could move to; these are all the cells within a radius that increases with the trout's length. The model trout then examines habitat conditions (including food consumption by larger trout) in these potential destination cells and calculates the growth rate and survival probability it would obtain in each cell, if it were either feeding or hiding there.

To make its selection of activity and habitat cell, a model trout evaluates four alternatives: feeding during the day and hiding at night, feeding both day and night, hiding during the day and feeding at night, and hiding during day and night. These alternatives are evaluated for each potential destination cell. The evaluation is based on the estimated probability of surviving both starvation and predation and the growth that the model trout would obtain. The model trout then selects the activity and the habitat cell that provide the highest estimated survival and growth. This approach to modeling activity and habitat selection is fully described, justified, and tested in a journal article (Railsback et al. 2005) prepared to support the analyses in this report. The journal article demonstrates that *inSTREAM-SD*, as applied to the Green River sites, could reproduce a variety of patterns representing how real trout have been observed to adapt their activity and habitat selection to environmental conditions.

2.3 STUDY SITES AND HABITAT INPUT

2.3.1 Study Sites

This study applied the trout IBM to four study sites that were established by the 1980s instream flow studies of Hann et al. (1991), which used the PHABSIM habitat modeling method (Bovee 1982). Cell geometry and hydraulics were developed from the earlier study's PHABSIM hydraulic model files. An important weakness of this simulation study is its reliance on the very limited habitat data produced by Hann et al. (1991). The results of *inSTREAM-SD* (like PHABSIM) depend very much on how well the actual river habitat is represented by the data describing the geometry and hydraulics of the habitat cells, which is largely a matter of how many transects are used and how closely they are placed. Whereas typical *inSTREAM* applications represent a site using 20–30 transects with cell lengths of 2–20 m, Hann et al. used only 6–10 transects spaced 34–82 m apart (Table 1).

2.3.2 Habitat Input

The PHABSIM data from Hann et al. (1991) were used to determine cell widths and to model how cell depth and velocity vary with flow. For each transect, the PHABSIM data include a number of "stations," which are points along the transect where depth and velocity were measured at several flows. In the across-channel direction, the habitat cells for *inSTREAM-SD* are bounded by the midpoints between stations, so that each cell has one PHABSIM station near its center. The depth and velocity for that station are applied to the whole cell.

RHABSIM, a commercial version of PHABSIM (T.R. Payne Assoc., Arcata, California), was then used to calibrate cell hydraulics for *inSTREAM-SD*. Cell depths were modeled using a regression relationship between water surface elevation and flow, fit from the three calibration flows (approximately 25, 70, and 110 m^3/s) measured in the PHABSIM study. Cell velocities were modeled using a single flow approach: for each of the three calibration flows, a bed roughness factor was estimated and used to model velocities over a range of flows around the calibration flow.

TABLE 1 Study Site Characteristics

Site	Site Length (m)	Location, Distance Downstream from Flaming Gorge Dam (km)	Number of Transects in PHABSIM Model	Mean Cell Length (m)
Tailrace	204	0.5	6	34
Pipe Creek	482	2.4	10	48
Little Hole	404	11.3	6	67
Indian Crossing	494	16.1	6	82

The very long PHABSIM cells were divided longitudinally into multiple cells for the trout model. This change helps avoid potential artifacts of the long cells on fish simulations and allowed greater variation in the cell variables other than depth and velocity. Each PHABSIM transect was essentially split into several that have identical depth and velocity characteristics but length of no more than 20 m. For example, a PHABSIM transect with cells 67 m long was divided into 4 transects with cell lengths of 20, 20, 20, and 7 m. The model uses 19 transects and 668 cells to represent the Indian Crossing site, 21 transects and 577 cells for Little Hole, 26 transects and 655 cells for Pipe Creek, and 21 transects and 449 cells for Tailrace (some cells are dry except at extremely high flows).

Cells in *inSTREAM-SD* have several habitat variables that are assumed constant: the fraction of the cell with velocity shelters for feeding, the fraction with spawning gravel (not used in this study), the fraction with hiding cover, and the average distance a trout must move to find hiding cover. Values for these variables were not available from the PHABSIM study, so they were estimated via field observations made by the authors of this report in October 2001. During the field observations, the ways these variables changed over whole sites was sketched onto maps, and the maps were then used to estimate the values for each cell.

2.3.3 Habitat Variation among Study Sites

The four study sites were those used by Hann et al. (1991) to represent the habitat diversity of the Flaming Gorge Dam tailwater, and there are some clear differences among the sites in physical habitat. How the mean depth (Figure 1), velocity (Figure 2), and width (Figure 3) of each study site vary with flow was calculated from the trout model for low to moderate flows. The Pipe Creek site is distinctly deeper and slower, on average, than the other sites; this is due primarily to a large pool at its downstream end. The Tailrace and Little Hole sites are relatively shallow (but with average depth greater than 1 m at most flows). The Tailrace site is dominated by riffle habitat, so its velocities are higher at low flow, but increase less as flow increases.

The cell habitat variables estimated in the field reflect differences among sites that may be as important as the depth and velocity differences (Table 2). The Indian Crossing site stands out as having lower availability of velocity shelters and hiding cover. The Little Hole and Tailrace sites have much higher availability of velocity shelters, but Tailrace has relatively low hiding cover availability.

2.4 TIME-SERIES INPUT: FLOW, TEMPERATURE, AND FOOD CONCENTRATION

The time-series input data that define the flow scenarios analyzed in this report are daily temperatures and hourly flows. The concentration of drift food can also vary daily or hourly and is assumed to depend on temperature and (in some analyses) flow. This section describes how input data for these variables were developed.
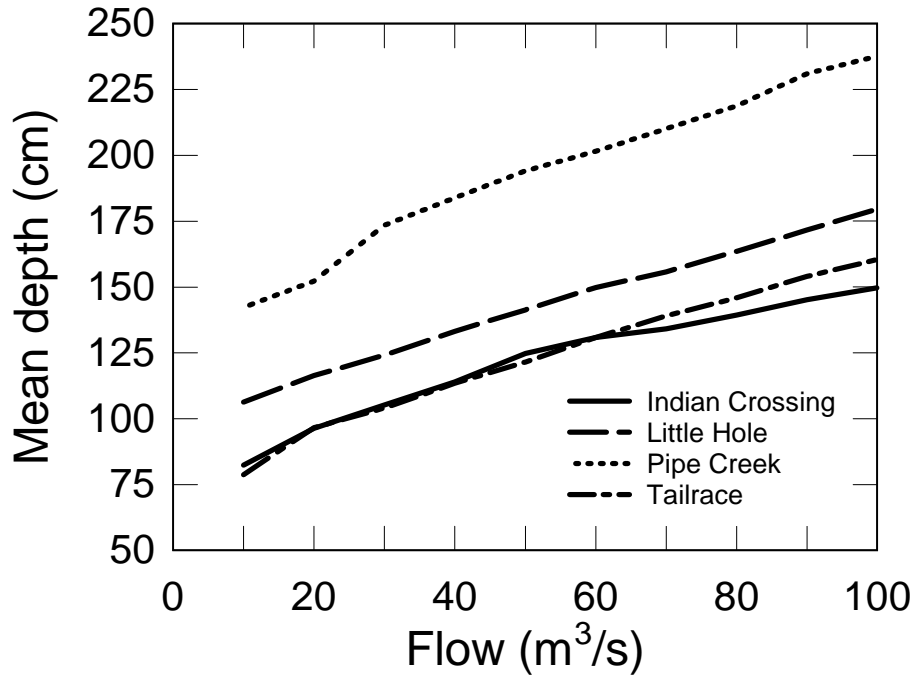
**FIGURE 1 Mean Depth as a Function of Flow from the *inSTREAM-SD*
Model for Each Site**
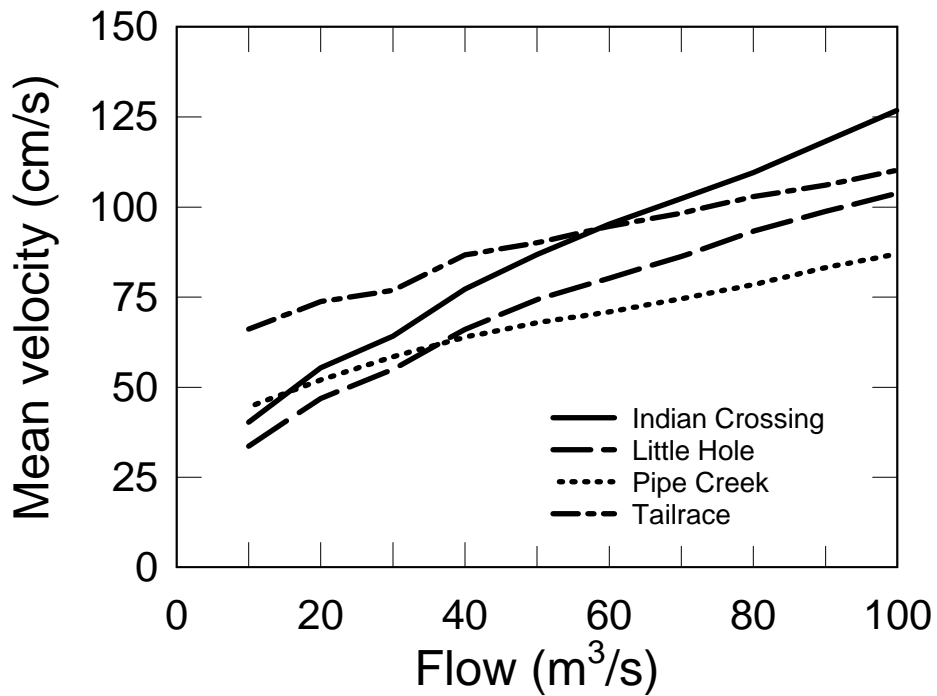
**FIGURE 2 Mean Velocity as a Function of Flow from the *inSTREAM-SD*
Model for Each Site**
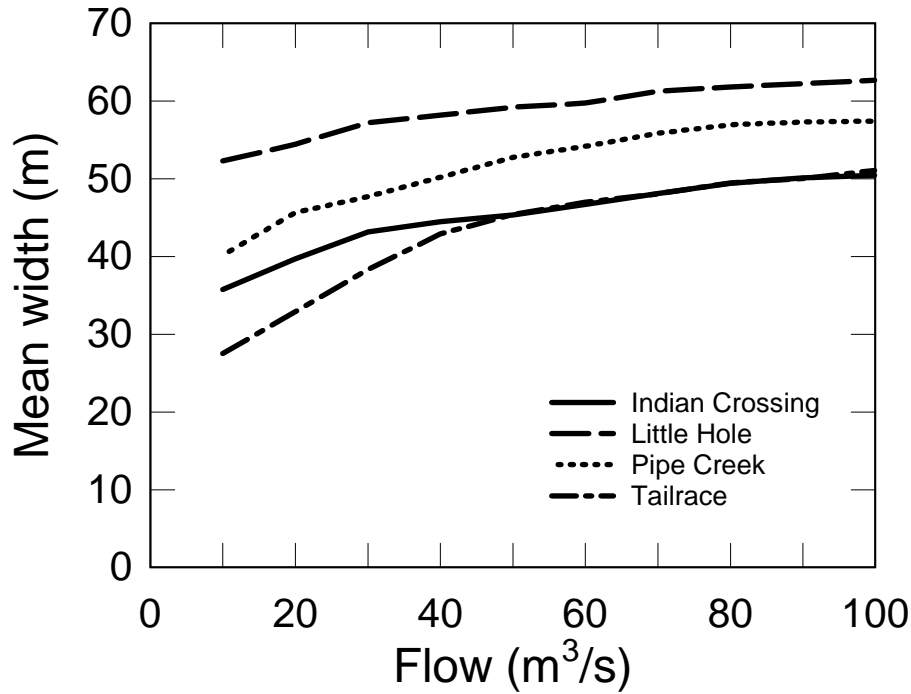
FIGURE 3 Mean Width as a Function of Flow from the *inSTREAM-SD* Model for Each Site

TABLE 2 Mean Cell Habitat Variables for Study Sites

Site	Fraction of Cell with Velocity Shelters	Distance to Hiding Cover (m)	Fraction of Cell with Hiding Cover
Tailrace	0.13	3.7	0.09
Pipe Creek	0.07	2.6	0.18
Little Hole	0.13	1.4	0.27
Indian Crossing	0.03	6.9	0.01

2.4.1 Flow

Flow input was developed considering (1) the objective of analyzing alternative flow management scenarios instead of examining actual historic flows, (2) the general patterns of seasonal flow recommended in the recent instream flow recommendations below Flaming Gorge Dam (Muth et al. 2000), and (3) observed year-to-year variation in inflow to Flaming Gorge Reservoir and reservoir releases. As a result of these considerations, three baseline flow scenarios were developed to represent dry, average, and wet years.

The flow scenarios are quite simple. Daily mean flows are constant "base flows" year-round except for a period of seasonal "peak flows" (the terminology used by Muth et al. 2000) in late May through mid-June. The seasonal peak flows increase over several days, plateau, then

decrease over several days; the magnitude and duration of the peaks vary among year types. These seasonal peaks are shown in Figure 4; during the rest of the year, the daily mean flow is equal to the values shown as occurring before May 24 and after June 21.

The within-day flow fluctuation scenarios are described along with their analysis in Sections 2.7 and 4.

2.4.2 Temperature

A simple approach to temperature input was used. Predicting how daily water temperatures would vary with flow release scenarios would require an elaborate reservoir modeling exercise and could make trout model results more difficult to understand. Instead, temperature was largely eliminated as a source of variation among scenarios in the study results. Monthly mean values were used as daily values (e.g., for each day in April, the temperature input was equal to the April mean value).

The monthly mean values were developed from data recorded in calendar year 2003. Earlier historic data were not included, because they would not reflect the recent management change to increase summer release temperatures. (Flaming Gorge Dam's selective withdrawal structure is now operated to release 12–13ºC water from June through October.) Reservoir inflows were low in 2003, so the temperatures recorded that year do not include artifacts of high-flow events (although they could be affected by low reservoir storage levels). Data were available from temperature gages at the Tailrace site (Bureau of Reclamation) and from Browns Park (U.S. Fish and Wildlife Service); Browns Park temperature gages are approximately twice as far downstream from the dam as Indian Crossing.
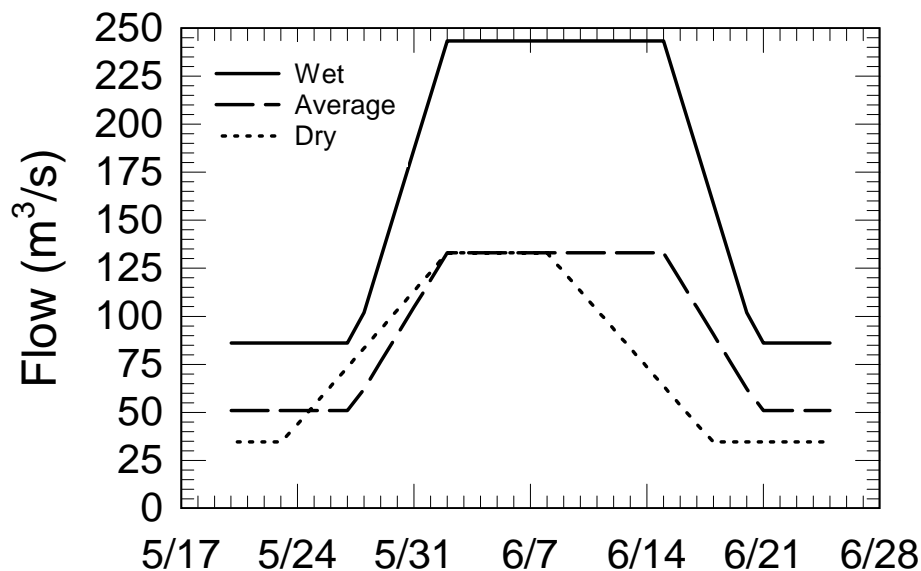
FIGURE 4 Seasonal Peak Flows for Dry, Average, and Wet Years

Data recorded at the Tailrace site were averaged to use as input for the Tailrace, Pipe Creek, and Little Hole sites (Table 3). At these sites, the combination of short distance downstream from the dam and high shading makes it reasonable to assume that the temperature is approximately equal to the reservoir release temperature. (Typically, releases from Flaming Gorge Dam are colder than air temperatures in summer and warmer than air temperatures in winter, so water equilibrates to the air temperature as it flows downstream.)

The Indian Crossing site was considered far enough downstream that a separate temperature input was developed for it, using the Browns Park data. The difference in temperature between the Tailrace and Browns Park areas was found to depend on flow. Therefore, monthly temperatures at Indian Crossing were modeled as the mean of Tailrace and Browns Park monthly temperatures, with the Browns Park temperature varying among dry, average, and wet flow year types (these year types are defined below). How Browns Park monthly water temperatures vary with monthly mean flow was determined via regression analysis of data from 1988 to 2003. However, these historic data do not reflect the recently implemented increases in summer release temperatures. To account for these increases, 1°C was added to the calculated Indian Crossing temperatures for June, September, and October, and 2°C was added to July and August temperatures (Table 3). These summer temperature increments are supported by the 2003 data.

2.4.3 Drift Food Concentration

The concentration of invertebrate food for drift-feeding trout was assumed to be proportional to water temperature. (In Section 5, alternative assumptions about how flow affects drift concentration are also examined.) This assumption is supported by the field observations of

TABLE 3 Monthly Mean Temperatures (°C) Used as Daily Input

| | Tailrace, Pipe Creek, | Indian Crossing | | |
Month	Little Hole	Dry	Average	Wet
January	4.5	3.6	3.8	4.6
February	4.4	3.7	3.8	4.1
March	4.6	4.8	4.8	4.8
April	5.5	7.0	6.8	6.2
May	8.6	10.4	10.2	9.5
June	12.4	13.2	13.1	13.0
July	12.5	15.0	14.7	13.8
August	12.7	14.6	14.4	13.8
September	12.8	13.4	13.4	13.4
October	12.1	11.3	11.4	11.6
November	8.1	7.3	7.5	8.1
December	6.3	4.6	4.9	5.7

Filbert and Hawkins (1995), who measured drift concentrations at four times of the year at the Tailrace and Little Hole sites. Their data show a coarse proportional relationship between drift concentration and temperature (Figure 5). Preliminary calibration of the trout model indicated that constant drift concentrations of 1.5×10^{-10} g/cm^3 produced reasonable trout growth and behavior. Therefore, drift concentration input was developed by assuming that concentration is proportional to temperature, with the annual mean concentration equal to 1.5×10^{-10} g/cm^3.

2.5 INITIAL POPULATIONS

Simulations were initialized by specifying the number and mean fork length of trout in each of seven age classes. Initial trout sizes were assumed constant among study sites, but the number of initial trout varied among sites to reflect site differences in both habitat area and observed trout density. Initial population characteristics were estimated using data from the Utah Division of Wildlife Resources (UDWR) annual fish censuses, which are usually conducted in the spring and fall. The UDWR data from 1997 to 1999 include the observed age and total length[1] of individual trout, so they are useful for estimating the relative abundance and mean size of the different age classes. Age class characteristics of the initial population are shown in Table 4.
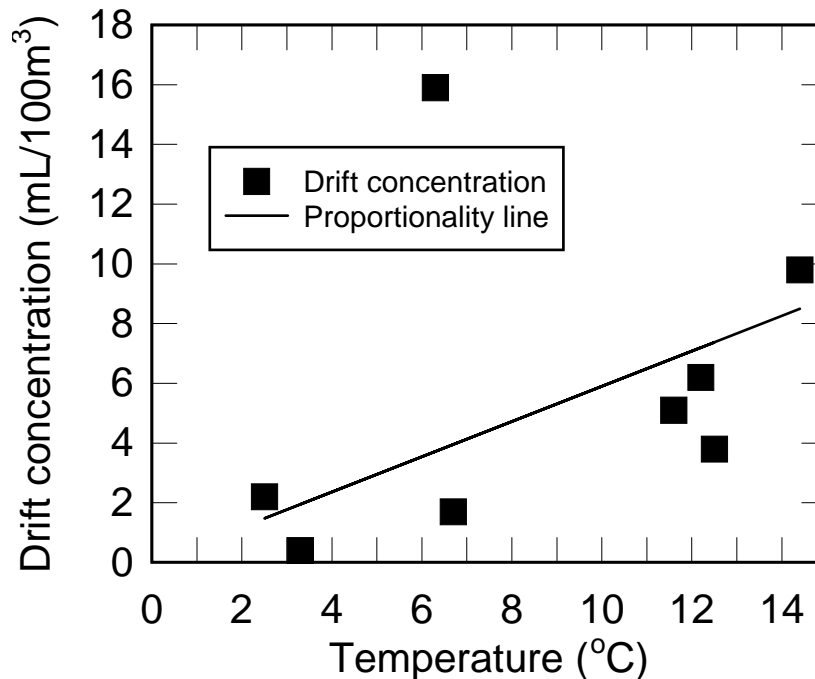
FIGURE 5 Drift Concentrations as a Function of Temperature as Reported by Filbert and Hawkins (1995)

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[1] Total length was converted to fork length using relationships provided in Carlander (1969).

UDWR does not consider its data to be reliable for estimating trout densities. Therefore, initial abundances were based on the trout biomass densities reported—but not documented—by Filbert and Hawkins (1995), with the UDWR data on age class mean biomass being used to estimate typical abundance densities at each site. Filbert and Hawkins reported biomass densities of 84 g/m^2 at Tailrace and 50 g/m^2 at Little Hole. From these values, the Pipe Creek biomass density was approximated as 67 g/m^2 (the average of Tailrace and Little Hole, as Pipe Creek is between these two sites) and that for Indian Crossing as 42 g/m^2 (half the Tailrace value). The initial abundances used in model analyses (Table 5) were determined as the number of trout that produce these biomass densities, with the age structure depicted in Table 4.

2.6 STOCKING

Populations of rainbow trout (the most common species) in the study reach are sustained largely by stocking of large hatchery fish. Stocking was represented in the simulation analyses, while natural spawning was not. Representing replenishment of adult populations through stocking is important because it can strongly affect how trout production is affected by flow changes, in that unless populations are replenished, fewer fish are forced to use less-optimal habitat where flow effects may be stronger. Natural spawning was not represented, because it is considered relatively unimportant below Flaming Gorge Dam and because, in our one-year

TABLE 4 Age Class Characteristics of the Initial Population

Age Class	Abundance (% of total population)	Length (mean standard deviation, cm)
0	2	12 (1)
1	13	26 (4)
2	21	28 (4)
3	19	35 (4)
4	20	39 (3)
5	29	41 (3)
6	6	42 (4)

TABLE 5 Initial Population Abundances

Study Site	Site Area at 60 m^3/s Flow (m^2)	Initial Trout Biomass (g)	Number of Initial Trout
Tailrace	9,600	806,000	1,050
Pipe Creek	26,100	1,750,000	2,900
Little Hole	24,000	1,200,000	2,000
Indian Crossing	23,100	970,000	1,050

simulations, it would have relatively little effect on population production (the output that was analyzed) while greatly increasing computations.

Stocking was represented using input values for the date, number, mean length, and standard deviation in length of each stocking event. Historic stocking records from UDWR were used to estimate these inputs.

Stocking was assumed to occur once during the one-year simulation period, on June 15, at all sites except Indian Crossing (UDWR does not stock trout at this location). The stocked fish were assumed to have a mean length and standard deviation of 19.3 cm and 1.6 cm, respectively. The assumed number and corresponding biomass of stocked trout are reported in Table 6. This table also reports the biomass of stocked trout as a percent of the January 1 population biomass used as a starting point for trout production results.

2.7 SIMULATION EXPERIMENTS: TIME PERIOD AND OUTPUT

The analyses of fluctuating flow effects use simulation of a one-year time period, starting on January 1. To reduce the effects of initial conditions, the model was started at the previous September 1 for a four-month period. During this initial period, the same flow and temperature inputs were used as for the following year of analysis simulations.

The results used as analysis endpoints are the simulated production of the trout population between the January 1 starting date and the December 31 ending date. Production is defined as the increase in total population biomass from January 1 to December 31, minus the biomass added via stocking. Production is reported as a percent of the starting biomass, which makes the results comparable among study sites, which vary in starting biomass.

To be precise, the production output is calculated by (1) multiplying the January 1 number of trout in each age class by the January 1 mean weight of each age class, and summing to get the total population biomass at the start of the simulation; (2) multiplying the December 31 (final) number of trout in each age class by the December 31 mean weight of trout in the age class, and summing these to get the total population biomass at the end of the simulation; (3) subtracting the starting biomass from the ending biomass; (4) subtracting the biomass added

TABLE 6 Abundance and Biomass of Stocked Trout

Study Site	Number of Stocked Trout	Biomass of Stocked Trout (g)	Biomass of Stocked Trout as Percent of Initial Trout Abundance (%)
Tailrace	566	57,000	10
Pipe Creek	1,336	134,000	7
Little Hole	1,120	113,000	8
Indian Crossing	0	0	0

via stocking, to get the increase in biomass; and (5) dividing the increase in biomass by the starting biomass, to get production as percent of January 1 starting biomass.

Production therefore increases as the average growth of the trout increases, but is decreased by mortality. Under many scenarios, production is negative, meaning that the loss of biomass due to mortality was not made up by growth of the surviving trout. However, simulated production should be treated as an index of overall trout production conditions under alternative scenarios, not as a testable prediction of trout populations (Section 2.1).

The results of *inSTREAM-SD* are stochastic to some extent, in that re-running the same scenario can produce different results, because some events in the model (especially, setting the length of individual fish in the initial population and in stocked fish, and trout mortality) are determined by pseudorandom numbers. "Replicate" simulations use the same input scenario but different pseudorandom numbers, and can be used to quantify the degree to which results are stochastic. In general, the results presented here would differ stochastically from replicates only by relatively small amounts (approximately 5 to 10%).

2.8 PRELIMINARY EXPERIMENTS TO EXPLORE MODEL SENSITIVITIES

This section describes several exploratory simulation experiments. The experiments were conducted in part to understand how sensitive the model results are to important inputs, and also because they help explain the results of the simulation experiments in Sections 3 to 5.

2.8.1 Trout Production vs. Base Flow

This experiment examined how trout production at each study site varied with base flow. The flow scenarios tested in this experiment were the average year with no within-day flow fluctuation, except that a wide range of base flows (flows during all of the year except the seasonal peak; Section 2.4.1) were tested. The results therefore indicate how simulated trout production conditions vary with flow in the absence of within-day flow fluctuations.

This experiment shows that Pipe Creek and Little Hole populations respond very similarly to base flow (Figure 6): production increases with flow up to a peak of about 50 m^3/s, then decreases gradually at higher flows. Production at Indian Crossing is low and relatively insensitive to flow. The low availability of velocity shelters for feeding likely explains why production at Indian Crossing peaks at a lower flow than at other sites, and the low availability of either deep water or hiding cover likely produces relatively high predation mortality. Results for the Tailrace site are more complex: production is predicted to spike sharply between 35 and 40 m^3/s, then decrease, and start increasing again at about 60 m^3/s. The spike was confirmed by additional model runs (not shown here) to not be a stochastic artifact. Instead, this spike could reflect actual hydraulic complexities of the Tailrace site or (more likely) could be an artifact of the very limited data (six PHABSIM transects) available to model the site's hydraulic habitat (Section 2.3.2). The effects of this spike will be seen in the results of subsequent experiments.
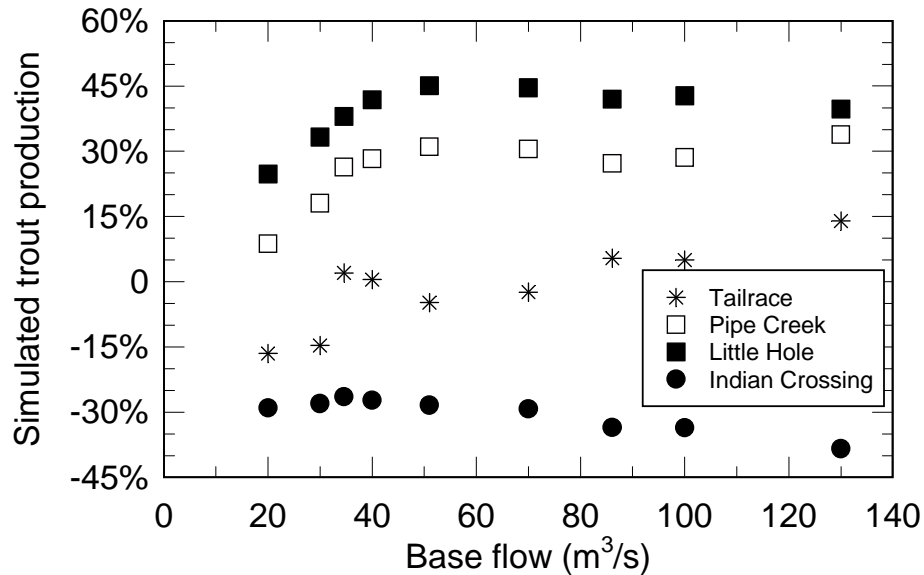
FIGURE 6 Response of Simulated Trout Production to Base Flow

2.8.2 Effect of Feeding Penalty Time

Section 2.2.2.1 discusses the "feeding penalty time," a parameter used to represent a hypothesized effect of flow fluctuations on trout growth—that when fish move in response to flow changes, their chosen activity (feeding or hiding) is disrupted. The penalty time parameter is the amount of time (in hours) that feeding or hiding stops if a fish moves during a time step. No literature or field observations could be found to support a value for this parameter, so a value of 0.25 h was assumed. This experiment examined the importance of this parameter by comparing model results with three different values. The value of 0.25 h is considered conservatively high, so it was compared to the smallest possible value (0.0 h), an intermediate value (0.125 h), and a very high value (0.5 h).

The experiment used the single daily flow fluctuation scenarios examined in Section 3. The Little Hole site was used because it is a large site with more diverse habitat than the other sites. Only the average flow year was examined.

Results of the sensitivity experiment on feeding penalty (Figure 7) show one qualitative difference between a value of zero (no effect of moving on feeding efficiency) and the other values. When the feeding penalty is zero, trout production was essentially unchanged with flow fluctuations at least as high as 25% of full load-following; with positive values of the feeding penalty, even small fluctuation magnitudes produce some decrease in trout production.

However, Figure 7 also shows that the size of the feeding penalty parameter should have little effect on the experiments in this report. Of most concern is the relationship between fluctuation magnitude and trout production. Increasing values of feeding penalty shifted the relationship downward but made negligible changes in its slope. For the four values of feeding
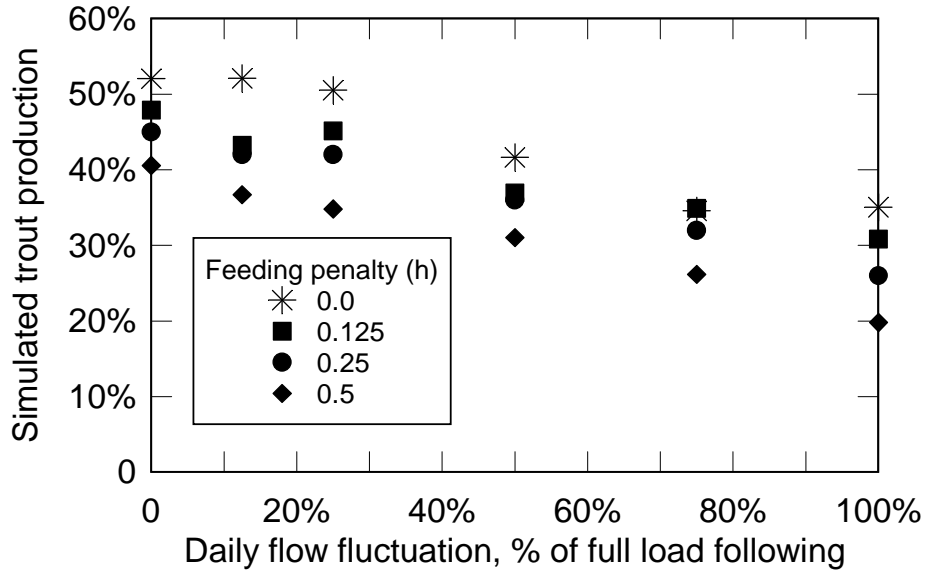
FIGURE 7 Sensitivity of Simulated Trout Production to Feeding Penalty Parameter Value at the Little Hole Site in an Average Year

penalty (from 0.0 to 0.5), the slopes of the regression line for trout production vs. fluctuation magnitude are –0.21, –0.17, –0.19, and –0.20. In other words, the effect of the feeding penalty appears not to change as fluctuation magnitude changes.

3 EXPERIMENT 1: EFFECTS OF FLOW FLUCTUATION MAGNITUDE

The first experiment addresses this study's first objective: understanding how the magnitude of within-day flow fluctuations affects trout production. The experiment's design follows a sensitivity analysis approach: in a series of otherwise identical model runs; the magnitude of daily fluctuations is increased from none to high.

3.1 FLOW SCENARIOS

For each hydrologic year type (dry, average, wet), six flow scenarios were developed to represent typical single-peak daily load-following operations at Flaming Gorge Dam. The six scenarios have the same number of on-peak hours per day and the same daily mean flow, but vary in the magnitude of the peak.

Full load-following was defined as a flow of 133 m^3/s, which represents the maximum power plant capacity at Flaming Gorge Dam. Scenarios other than full load-following were defined by their percent of full load-following: their peak's magnitude as a percent of the difference between daily mean flow and 133 m^3/s. For example, in average years, the daily mean base flow is 51 m^3/s, so the 50% peak scenario has a peak flow of 92 m^3/s (50% of the difference between 51 and 133 m^3/s). Flows during off-peak hours are reduced in proportion to the peak magnitude to keep the daily mean flow constant among scenarios.

The six flow scenarios analyzed are 0, 12.5, 25, 50, 75, and 100% of full load-following. The different hydrologic year types have different mean flows and different numbers of hours of peaking per day (Table 7). These assumptions produce the hourly flows depicted in Figure 8 (dry years), Figure 9 (average years), and Figure 10 (wet years). Weekends were assumed to have the same load-following pattern as weekdays.

During the seasonal peak flows (Figure 4), flows are assumed not to fluctuate during the day; each hour's flow is equal to the daily mean.

TABLE 7 Daily Mean Flow and On-Peak Hours for Flow Fluctuation Scenarios

Hydrologic Year Type	Daily Mean Flow (m^3/s)	Number of On-Peak Hours
Dry	34.6	3
Average	51.0	6
Wet	86.1	14
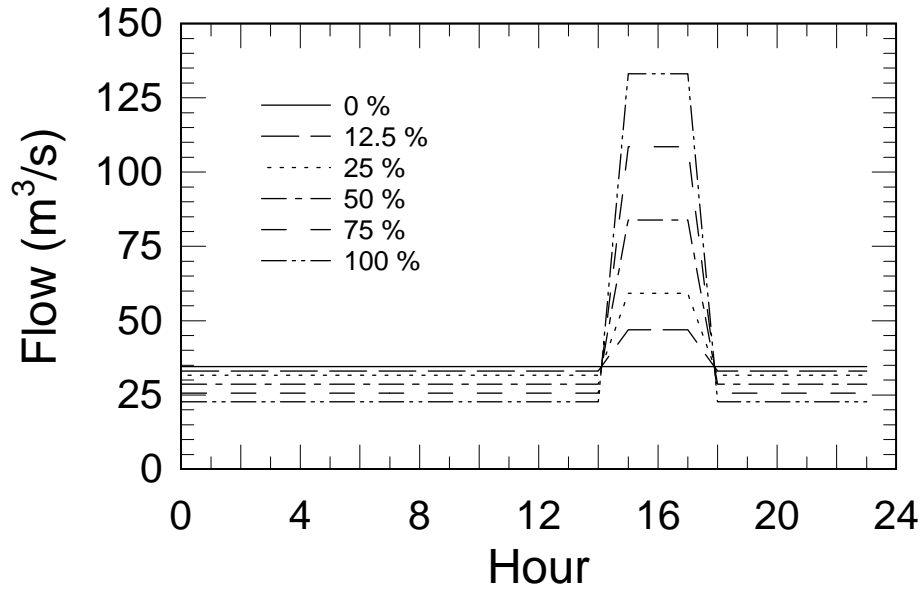
FIGURE 8 Hourly Flows for Single Daily Fluctuations in Dry Years
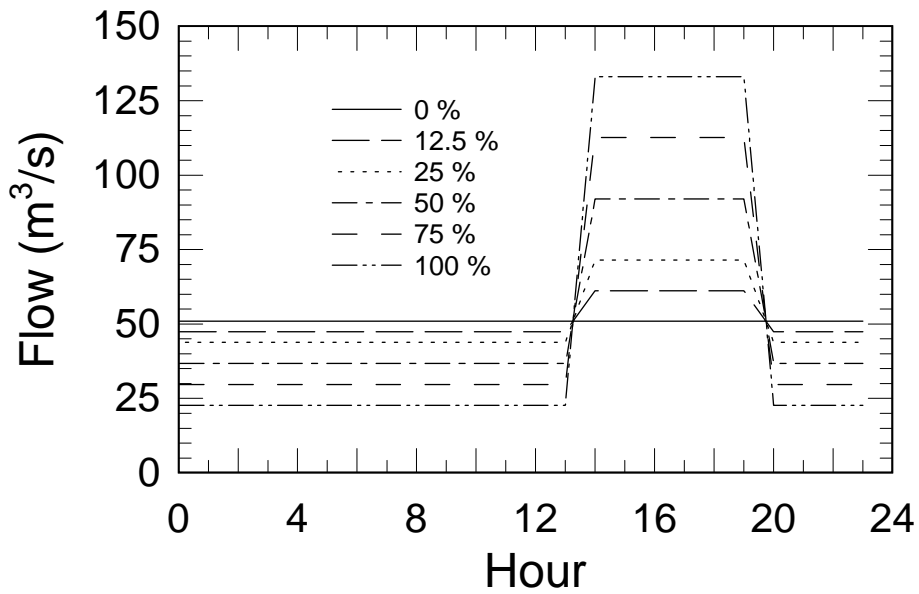
FIGURE 9 Hourly Flows for Single Daily Fluctuations in Average Years
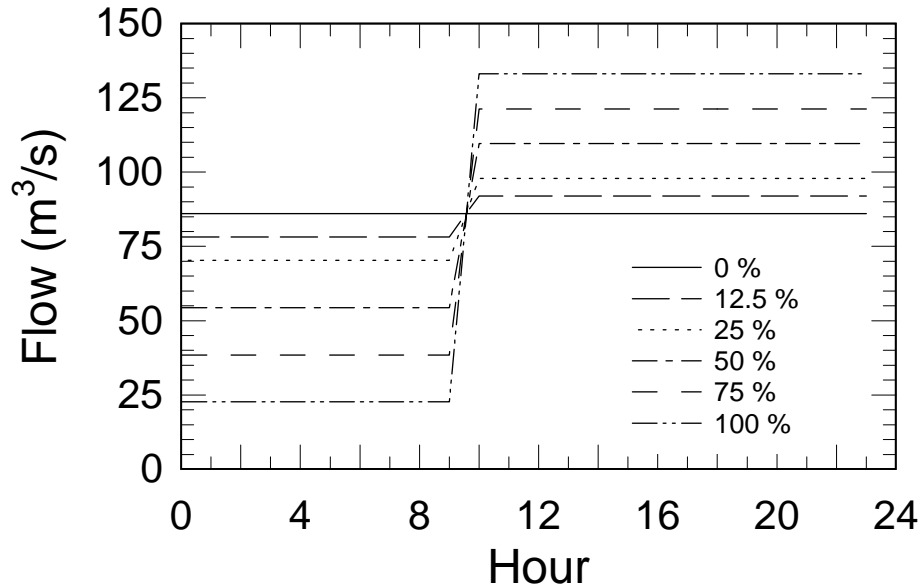
FIGURE 10 Hourly Flows for Single Daily Fluctuations in Wet Years

3.2 RESULTS

3.2.1 Effects of Fluctuation Magnitude on Trout Production

Predicted responses of trout populations to flow fluctuation magnitude are depicted graphically, with one figure for each study site. Simulated production at Indian Crossing, as percent of the initial biomass (Figure 11), is considerably lower than at other sites, at least partly because of the site's lower availability of feeding and hiding cover. Production generally decreases with increasing fluctuation magnitude, but not drastically, and there is little difference between low and moderate fluctuation magnitudes. The slope of a regression line for average years at the Indian Crossing site is low: –0.074. This slope means that increasing fluctuation magnitude from zero to 100% decreases trout production by 7%.

At Little Hole (Figure 12), production is high and decreases more with increasing fluctuation magnitude. The slope of a regression line for average year results is –0.18, thus, increasing fluctuation magnitude from 0% to 100% decreases trout productivity by 18%. The average-year regression line has a high correlation coefficient (r^2=0.99), indicating that the decrease in production is highly linear with fluctuation magnitude. Results for dry and wet years are less linear. Dry-year production is little affected by fluctuation at low magnitudes, but decreases relatively sharply at high fluctuation magnitudes. In contrast, wet-year production drops between zero and 12.5% fluctuation, but decreases very little as fluctuation magnitude continues to increase.
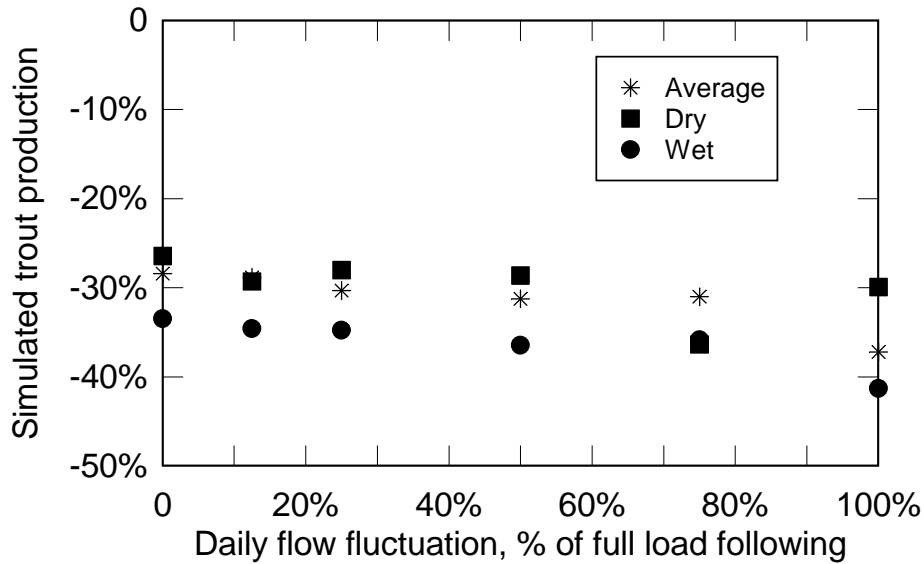
FIGURE 11 Simulation Results for Indian Crossing with a Single Daily Fluctuation
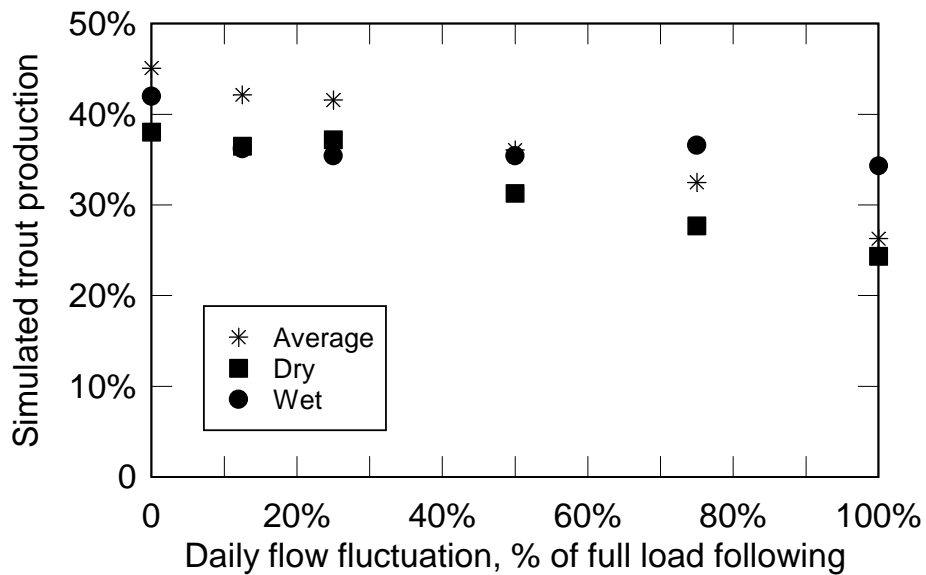
FIGURE 12 Simulation Results for Little Hole with a Single Daily Fluctuation

These results appear to be largely explained by interactions between the fluctuating flow scenarios (Figures 8 to 10) and the flow-production relationship for steady flows (Figure 6). Figure 6 shows that, for all sites but Indian Crossing, trout production conditions increase quite steeply with flow up to about 50 m³/s, and vary little at higher flows. The base flow for average years is, coincidentally, also close to 50 m³/s. As daily peaking magnitude increases, the off-peak flow drops lower and lower below 50 m³/s to maintain a constant mean daily flow

(Figure 9), likely explaining the linear decrease in trout production with increasing fluctuation magnitude in average years. In dry years, low fluctuation magnitudes provide peak flows in the >50 m^3/s range of optimal production, almost offsetting the lower flows in off-peak hours (Figure 8), whereas high-magnitude fluctuations push off-peak flows further down in the range (<30 m^3/s) where production decreases sharply with flow. In wet years, the drop in production between zero and 12.5% fluctuation is unexplained, but the lack of response to higher magnitude fluctuations could be because both on- and off-peak flows (Figure 10) remain within the range of high production. The exception is at 100% of full load-following, when off-peak flows are well below optimal.

Results for Pipe Creek (Figure 13) are quite similar to those for Little Hole, probably because the relations between steady flow and trout production for these two sites are similar in shape (Figure 6). An exception to this similarity is that Pipe Creek production increases with flow above 90 m^3/s, likely explaining why production increases with fluctuation magnitude (except at 100%) in wet years. For average year results at Pipe Creek, a regression line of production vs. fluctuation magnitude has a slope of –0.14 (r^2=0.93), so fluctuations have slightly less negative effect than at Little Hole.

Tailrace results (Figure 14) are more complex, because of the more complex relationship between base flow and trout production (Figure 6). That relationship has a local minimum at about 50 m^3/s, which explains why trout production in average years actually increases with fluctuation magnitude up to 50% of full load-following. These fluctuations move both on- and off-peak flows away from 50 m^3/s and into ranges where trout production is higher. However, at 75 and 100% fluctuations, off-peak flows are pushed into the <35 m^3/s range where production is much lower. Correlation of simulated production to fluctuation magnitude is not statistically significant (p>0.2) for average years.
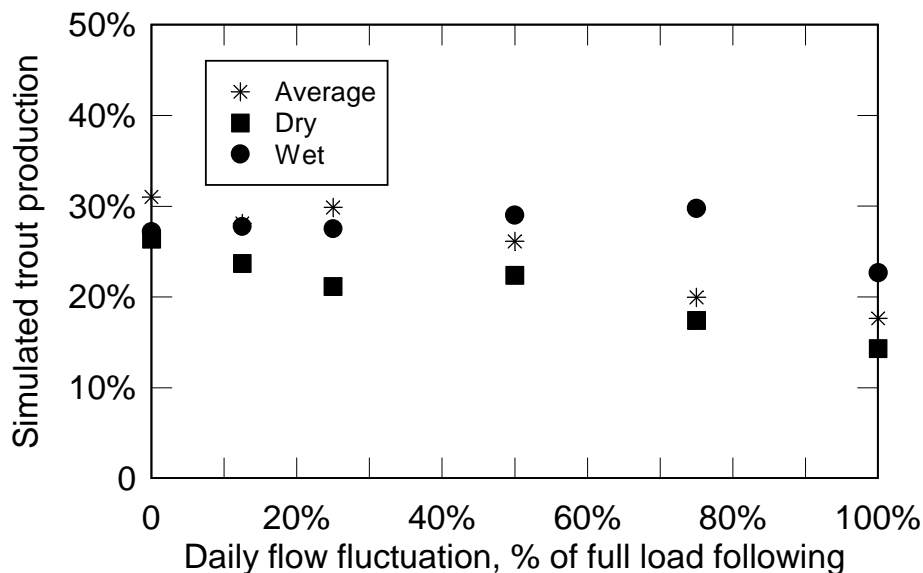
FIGURE 13 Simulation Results for Pipe Creek with a Single Daily Fluctuation
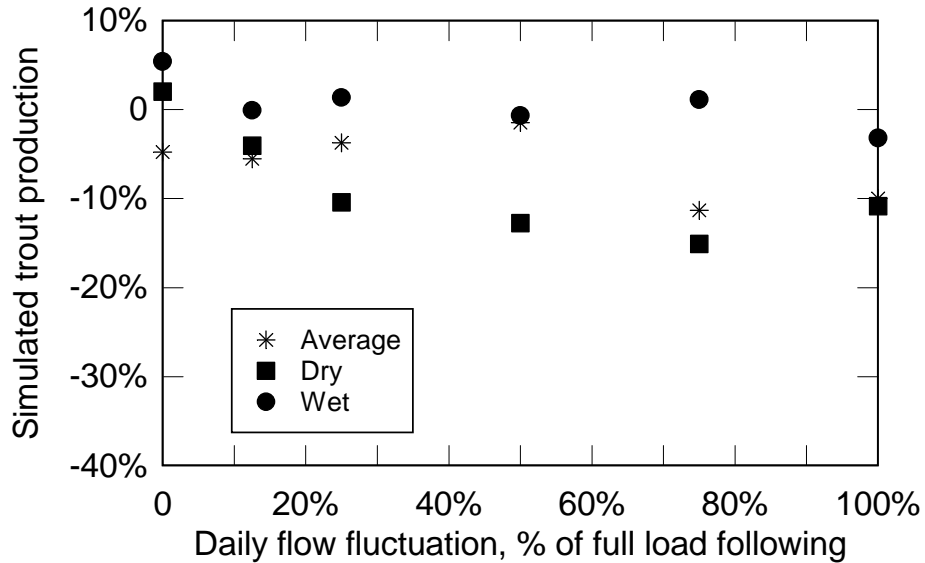
**FIGURE 14 Simulation Results for Tailrace with a Single
Daily Fluctuation**

In direct contrast to average years, wet years have a mean daily flow (86 m^3/s) very close to a local *maximum* in trout production (Figure 6). Consequently, increasing fluctuation magnitude generally results in slight decreases in trout production in wet years.

Dry year trout production is predicted to drop sharply with flow fluctuation magnitude, except at the highest magnitudes. As fluctuation magnitude increases, dry year off-peak flows are pushed further into the <35 m^3/s range where trout production at Tailrace is low.

3.2.2 Effects of Fluctuations on Trout Movement

Because one of the hypothesized effects of flow fluctuation is that it increases trout movement (Section 2.2.2.1), it is interesting to examine output for the distances trout moved under the different fluctuation scenarios. The *inSTREAM-SD* model reports the average distance that trout of each age class move for each time step. This output is the distance that simulated trout move among habitat cells in search of good places to feed or hide (it is *not* the distance that fish swim while foraging).

Figure 15 reports the average distance moved per day by trout in the age 3 and older class, which includes most of the simulated population. The distance moved generally increases with fluctuation magnitude, but changes little at fluctuations above 50% of full load-following. At full load-following, trout are predicted to move up to approximately twice as much as with no fluctuations.
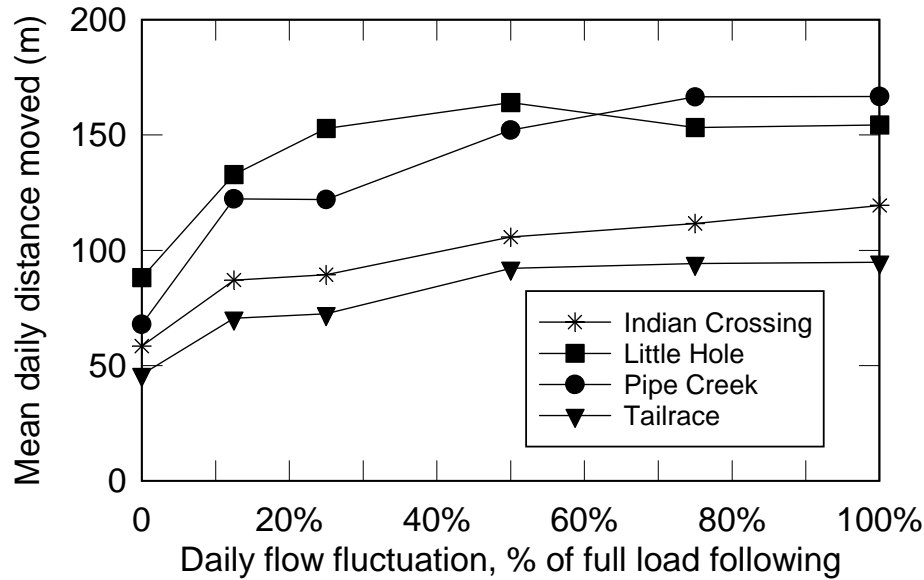
FIGURE 15 Mean Distance Moved by Age 3 and Older Trout during Single-Peak Simulations in Average Years

The additional movement resulting from flow fluctuations is very small compared to the distance trout swim while foraging. In all cases, simulated trout moved less than 200 m per day (Figure 15); a typical (40 cm) trout foraging at half its maximum sustainable swim speed (Railsback and Harvey 2001) would swim this distance in less than 7 minutes.

3.3 DISCUSSION FOR EXPERIMENT 1

The results of this experiment show, first of all, that effects of within-day flow fluctuation magnitude are neither consistent nor easily stereotyped. Fluctuation effects varied among sites and among hydrologic year types at each site. In some situations, increasing fluctuation magnitude resulted in higher simulated trout production, but more often it did not. In none of the scenarios did even full load-following result in catastrophic impacts on trout production.

The strongest patterns in simulation results can be explained as emerging from two relationships. First is the relationship between steady flow and trout production (Figure 6), which can be used as an indicator of how trout production varies with flow. The second relationship is the hourly flow patterns under each flow fluctuation scenario (Figures 8 to 10). Scenarios that provide more hours per day of flows that produce high trout production, as indicated by Figure 6, tend to increase trout production; scenarios that provide more hours per day of flows that are unsatisfactory for trout production produce lower production. This conclusion may appear fairly self-evident from this experiment, but it is not clear that fluctuation effects have been understood in this way before. Often, biologists have assumed that trout populations respond to the worst conditions occurring during a day instead of to the conditions occurring during most hours of the day. For dry and average years, when there are more off-peak and on-peak hours per day, this

experiment indicates that the effects of a fluctuation flow scenario are dominated by the off-peak flow.

The hypothesized feeding penalty, representing the assumption that moving in response to flow change disrupts a trout's feeding, appears to have a relatively constant and small negative effect on trout production. The assumption that, on average, there is a fixed period of non-feeding after each move is predicted by *inSTREAM-SD* to have little influence on how flow fluctuations affect trout production. This assumption causes all fluctuating flows to result in slightly lower trout production than would occur with no feeding penalty, but it does not cause trout production to decrease further as fluctuation magnitude increases. This issue is addressed further in Experiment 2.

4 EXPERIMENT 2: EFFECTS OF SINGLE VS. DOUBLE PEAKS

The second experiment analyzes differences in trout production resulting from double instead of single load-following peaks in flow. "Double peaking" (two peaks per day) allows power production to more closely match the daily electricity demand cycle, even with the same number of on-peak hours per day. This simulation experiment contrasts trout production resulting from two discrete operating alternatives—single vs. double peaking—while all other inputs are held constant.

There are two mechanisms in *inSTREAM-SD* that could produce differences between single- and double-peaked flow fluctuations. First is that doubling the number of flow changes per day could cause fish to move more often, incurring the feeding penalty time (Section 2.2.2.1) more often. Second is potentially changing the fraction of on-peak flows that occur during day vs. night; trout growth and mortality risks depend on whether it is day or night as well as on flow. Because *inSTREAM-SD* models how day length changes seasonally, the effect of double-peaking on the number of on-peak hours in daytime varies over the year. In dry-year scenarios, there are 104 *fewer* daytime on-peak hours per year with double peaking than under single-peaking operations. In average years, there are 88 *more* daytime on-peak hours with double peaking; in wet years, there are 323 more daytime on-peak hours with double peaking.

4.1 DOUBLE-PEAK FLOW SCENARIOS

The double-peak flow fluctuation scenarios used in this experiment are identical to the single-peak scenarios (Section 3.1) in base flow, on-peak flow, and number of on-peak hours per day. The only difference is that some of the on-peak hours are shifted from afternoon to morning to more closely meet electrical demand. The scenarios are shown in Figures 16 to 18.

4.2 RESULTS

Results of this simulation experiment were analyzed in two ways. First, simulated trout production and movement are plotted against fluctuation magnitude, as they were for Experiment 1. This allows identification of any qualitative differences in simulated population response to flow fluctuation caused by double peaking. Second, a statistical comparison is made of results from single-peak simulations to those from double-peak simulations. The statistical analysis was used to evaluate whether there are any significant differences resulting from the number of peaks within a day.

4.2.1 Graphical Analysis

The double-peak simulations produced patterns of trout production response to fluctuation magnitude very similar to those for single daily fluctuations (Figures 19 to 22).
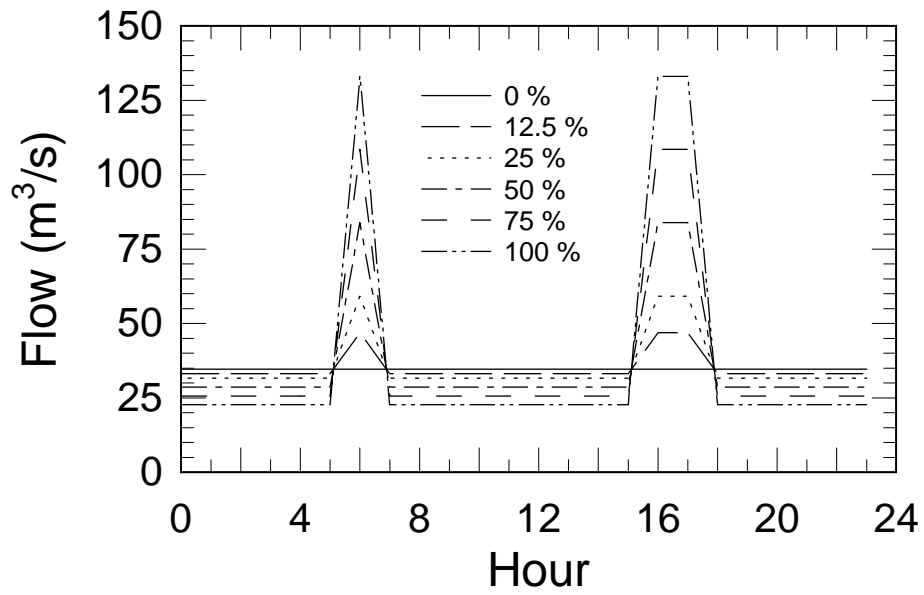
FIGURE 16 Hourly Flows for Double-Peaked Daily Fluctuations in Dry Years
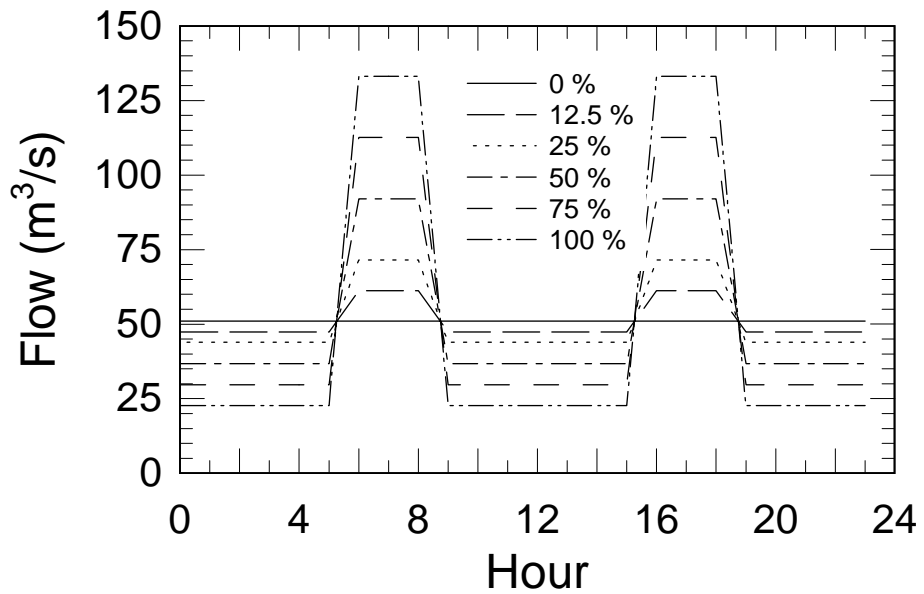
FIGURE 17 Hourly Flows for Double-Peaked Daily Fluctuations in Average Years
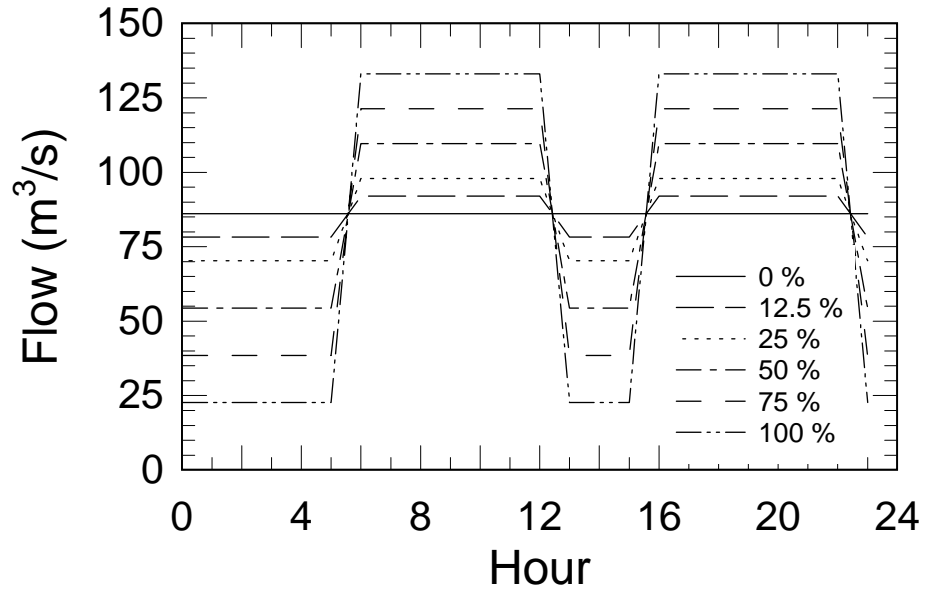
FIGURE 18 Hourly Flows for Double-Peaked Daily Fluctuations in Wet Years
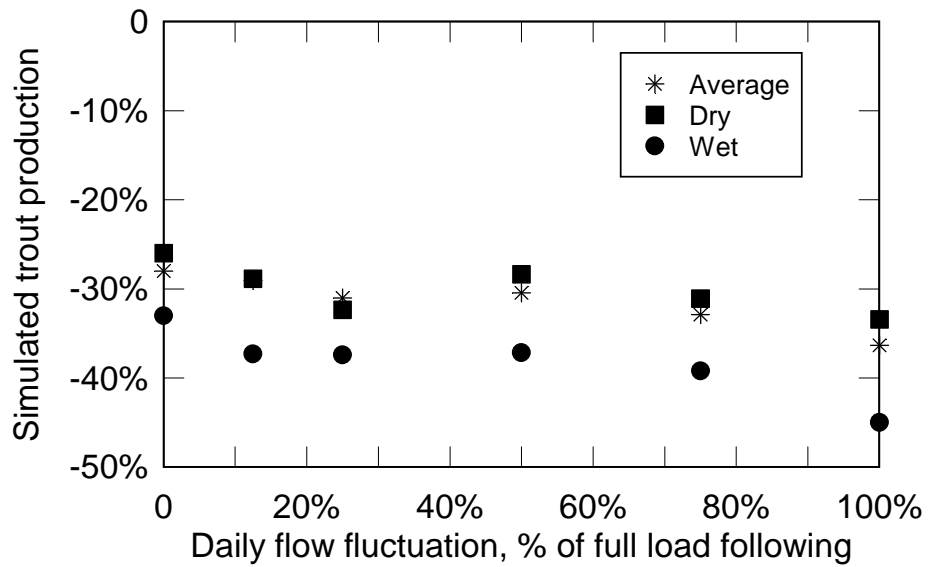
FIGURE 19 Simulation Results for Indian Crossing with Double-Peaked Fluctuations
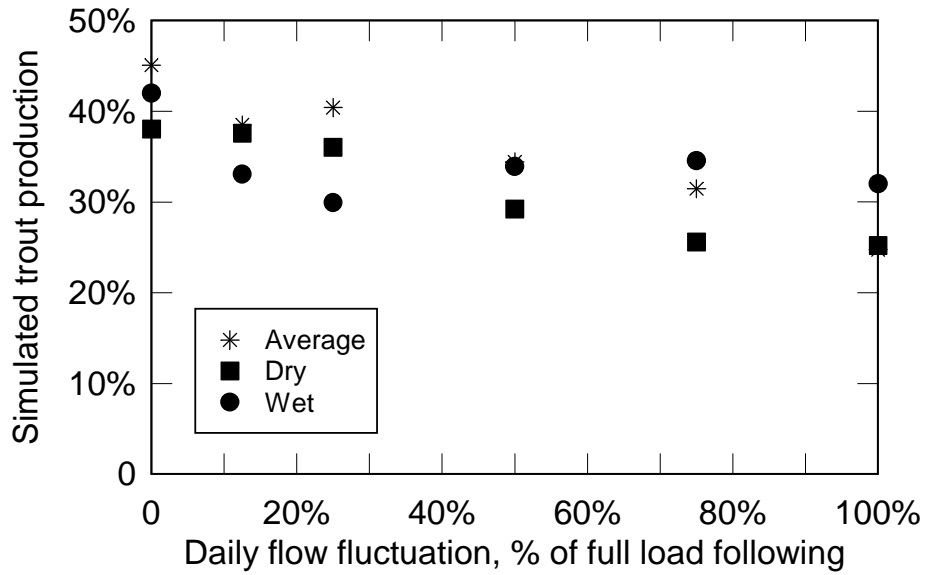
FIGURE 20 Simulation Results for Little Hole with Double-Peaked Fluctuations
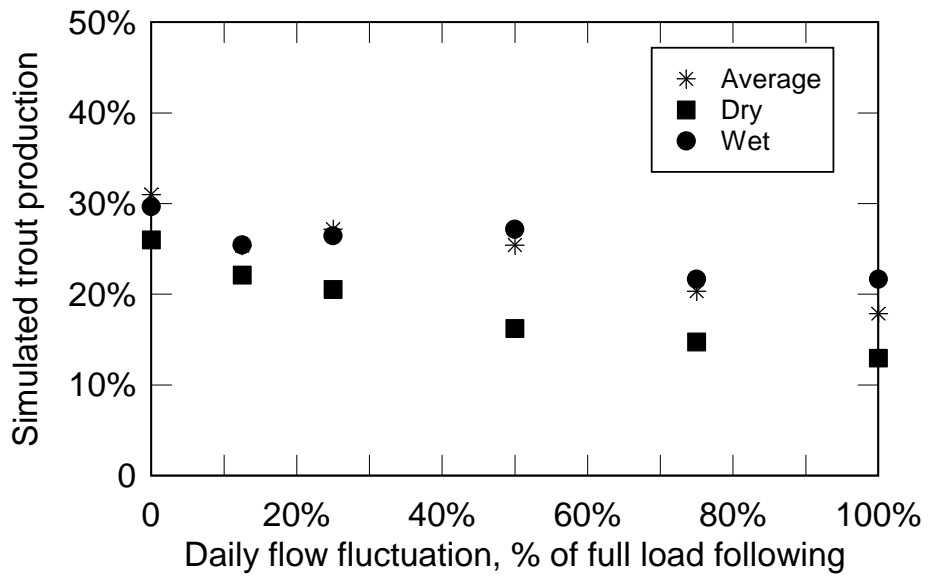
FIGURE 21 Simulation Results for Pipe Creek with Double-Peaked Fluctuations
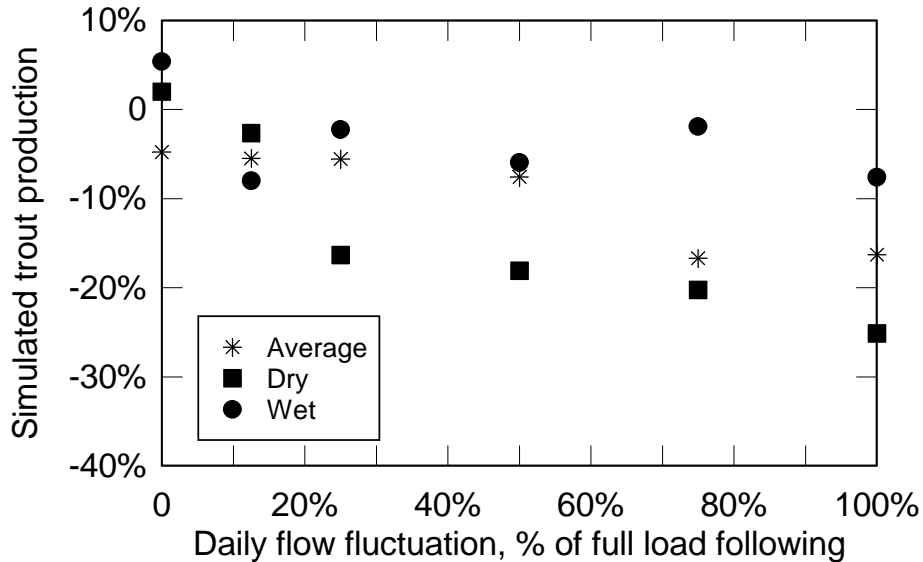
FIGURE 22 Simulation Results for Tailrace with Double-Peaked Fluctuations

All of the patterns discussed in Section 3.2 also appear in these figures, with a few minor exceptions (e.g., at Tailrace, average-year trout production decreases slightly at low fluctuation levels, whereas it increased slightly under single-peak operations). The slopes of regression relationships between simulated trout production and fluctuation magnitude differed little between single- and double-peak scenarios, except that at Tailrace a significant negative slope occurred only with double peaking (Table 8).

Graphical comparison of the average distance moved among cells by age 3 and older trout shows that double-peaking results in greater movement (Figures 23 to 26) than with single-peaking operation. This result is expected, as the number of flow changes per day is doubled. However, the distance moved under double peaking is at most 1.6 times the distance moved with single peaking. The predicted increase in movement due to double peaking remained less than 200 m per day (Figure 26).

4.2.2 Statistical Analysis

The statistical analysis used a one-sided, paired *t*-test to test the hypothesis that simulated trout production was lower in double-peak scenarios than in the otherwise identical single-peak scenarios. For each combination of study site, hydrologic year type, and fluctuation magnitude, results from single-peak simulations were compared to the corresponding double-peak results. All sites, year types, and fluctuation magnitudes were included in a single analysis. Zero-magnitude fluctuation scenarios were not included because there is no difference between single and double peaking. So there are 60 cases (4 sites × 3 year types × 5 fluctuation levels) included in the analysis.

**TABLE 8 Slope of Simulated Trout Production with Respect
to Fluctuation Magnitude for Single- and Double-Peaked
Fluctuations**

Study Site	Single-Peak Fluctuations	Double-Peak Fluctuations
Tailrace	Not significant	−0.13
Pipe Creek	−0.14	−0.11
Little Hole	−0.18	−0.18
Indian Crossing	−0.07	−0.07
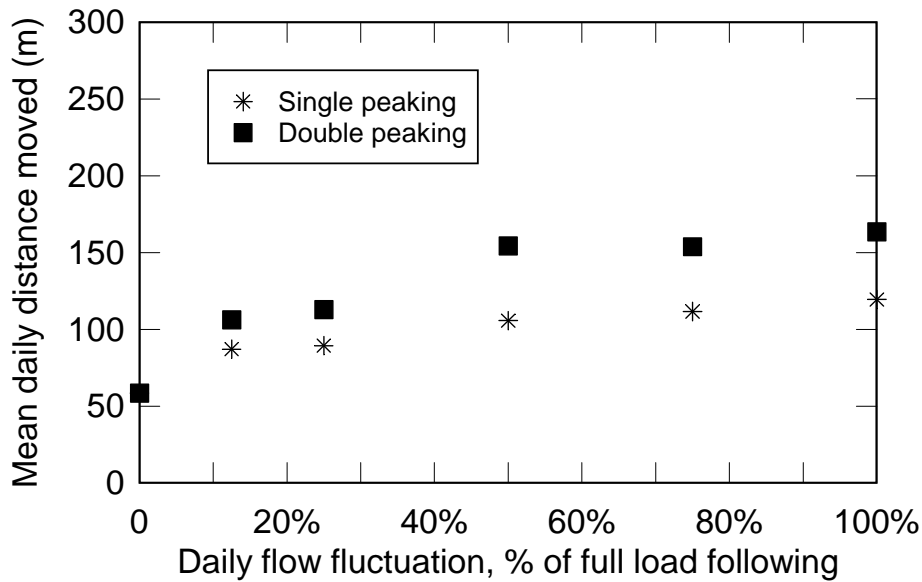
**FIGURE 23 Mean Daily Distance Moved by Simulated Age 3 and
Older Trout, with Single- vs. Double-Peaked Fluctuations in Average
Years at the Indian Crossing Site**

The *t*-test indicates that simulated trout production was consistently, but slightly, lower with double peaking than with single peaking. The difference was highly significant ($p<0.0001$), but the mean effect of double peaking was to reduce production by only about 2%. The 95% confidence interval on the effect of double peaking is 1.7–3.2%. This effect is relatively small in comparison to the biomass added via stocking (7–10%; Table 6).

4.3 DISCUSSION FOR EXPERIMENT 2

This experiment indicates that the most important effect of double peaking is related to the quality of habitat provided by off-peak flows. When the ability of trout to adapt to flow changes by moving is acknowledged, the effects of flow fluctuations can be predicted by looking
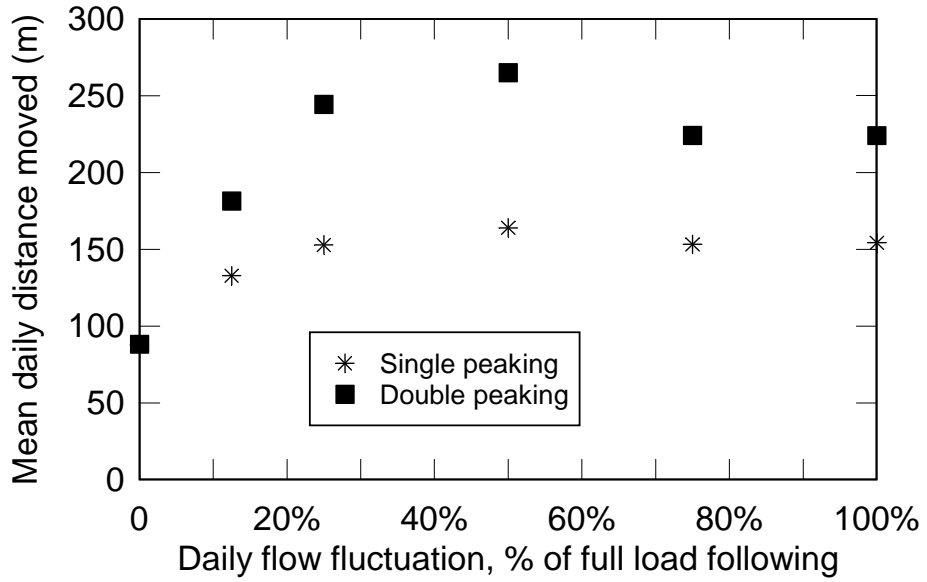
FIGURE 24 Mean Daily Distance Moved by Simulated Age 3 and Older Trout, with Single- vs. Double-Peaked Fluctuations in Average Years at the Little Hole Site
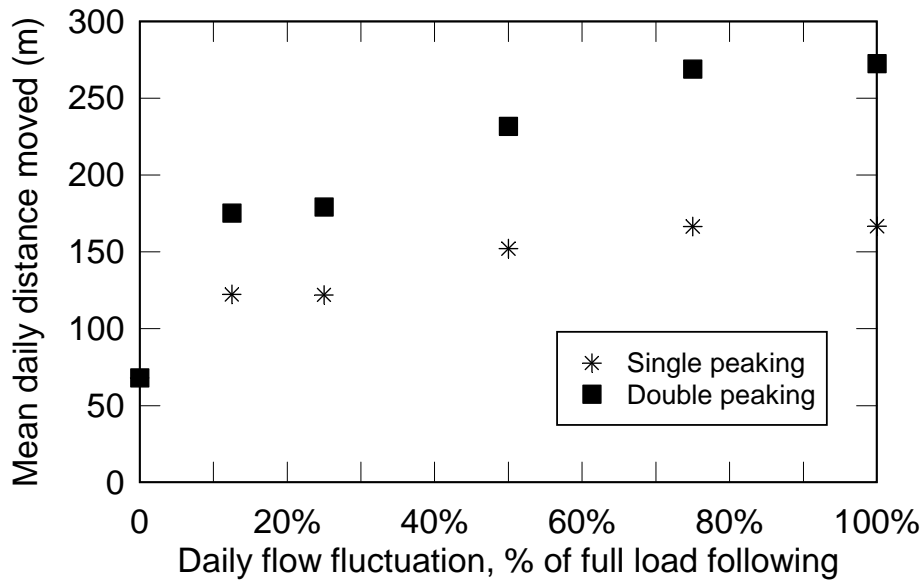
FIGURE 25 Mean Daily Distance Moved by Simulated Age 3 and Older Trout, with Single- vs. Double-Peaked Fluctuations in Average Years at the Pipe Creek Site
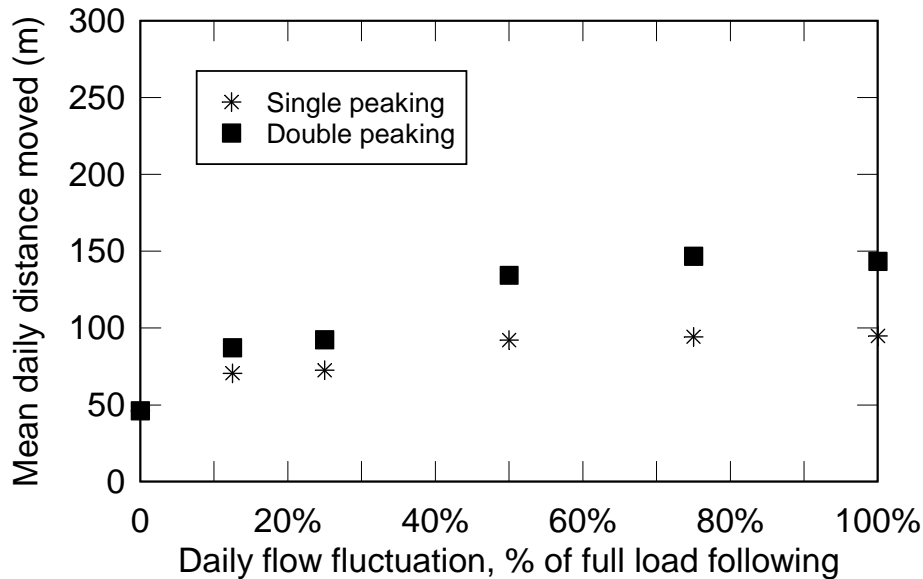
FIGURE 26 Mean Daily Distance Moved by Simulated Age 3 and Older Trout, with Single- vs. Double-Peaked Fluctuations in Average Years at the Tailrace Site

at the flows that occur during most of the day (the off-peak flows, during dry and average years) and whether those flows are relatively good or poor for trout production.

The experiment predicts a consistent but small negative effect of an additional flow peak per day. This difference in trout production between single and double peaking undoubtedly results from additional movement, and its magnitude depends on the assumed value of the feeding penalty parameter (Sections 2.2.2.1). The sensitivity experiment in Section 2.8.2 indicates that assuming trout feeding is disrupted less during movement would make the predicted effect of double peaking on trout production smaller (or, a higher feeding penalty would result in a greater predicted effect of double peaking).

Why does the model not predict that double-peaked flow fluctuations double the distance fish move or substantially reduce production, in comparison to single peaks per day? First, trout routinely move even when flow is steady; these moves are to switch between feeding and hiding behavior and to adjust to changes in conditions such as whether it is night or day, how many competing trout are nearby, and their own size and condition. The additional movement due to flow changes is (according to the model) not large compared to routine movement. Second, trout that are hiding instead of feeding are unlikely to be affected by flow changes, and are therefore less likely to move in response to them.

5 EXPERIMENT 3: EFFECTS OF FLUCTUATIONS ON INVERTEBRATE DRIFT

The objective of the third experiment is to investigate hypothesized effects of flow pulses on the food that trout eat and the consequences of those effects on trout production. Trout downstream of Flaming Gorge Dam appear to feed mainly on drifting macroinvertebrates, especially amphipods (*Gammarus lacustris*), mayflies (*Baetis* and *Ephemerella* spp.), caddisflies (*Hydroptila* spp.), and dipterans (blackflies and midges) (Filbert 1991; see also Filbert and Hawkins 1995).

5.1 HYPOTHESIZED EFFECTS AND SIMULATION SCENARIOS

Two mechanisms by which flow fluctuations could affect drift availability for trout have been hypothesized (1) changing the timing of drift within a day, and (2) changing the overall production of drift. The concentration of drifting invertebrates (in g/m^3) can be thought of as the balance between the rate at which invertebrates enter the drift from the benthos (in g/s) and the rate at which invertebrates are removed by feeding fish (also g/s), divided by the flow rate (m^3/s). Therefore, changes in flow can directly affect drift concentration: if the flow doubles while the rates at which invertebrates enter the drift and are eaten remain constant, the drift concentration is halved. Changes in flow can also change the rate at which invertebrates enter the drift: a tendency for invertebrates to drift more at higher flows can reduce or even reverse the reduction in drift concentration with increasing flow. The simulations in Experiments 1 and 2 used an intermediate assumption: the rate at which invertebrates enter the drift was assumed to increase in proportion to flow, so the drift concentration remained constant as flow changed.

No studies of how drift concentrations vary with flow have been conducted at Flaming Gorge Dam, but Leibfried and Blinn (1987) conducted such a study downstream of Glen Canyon Dam, a situation similar in many ways (including an invertebrate community made up largely of *Gammarus* and chironomids) to Flaming Gorge Dam. Leibfried and Blinn measured drift six times over a 24-hour period, once per month. The study period included five months of relatively steady flow releases (May–September 1985) followed by three months (October–December 1985) of load-following flow fluctuations with two peaks per day. Drift concentrations were reported as number of invertebrates per 100 ft^3 (2.83 m^3) of water, whereas *inSTREAM-SD* represents drift as invertebrate biomass per m^3. Re-analysis of data reported by Leibfried and Blinn (1987) indicate a weak positive relationship between flow and drift concentration during the period of fluctuating flow (Figure 27). (This relationship could in part result from flow peaks coinciding with times of day when invertebrates tend to drift naturally.) Figure 27 exhibits the variability that is typical of drift data. However, it does indicate that the most likely alternative to assuming drift concentration is not related to flow is that drift concentration increases, not decreases, with flow during periods of fluctuating dam releases.
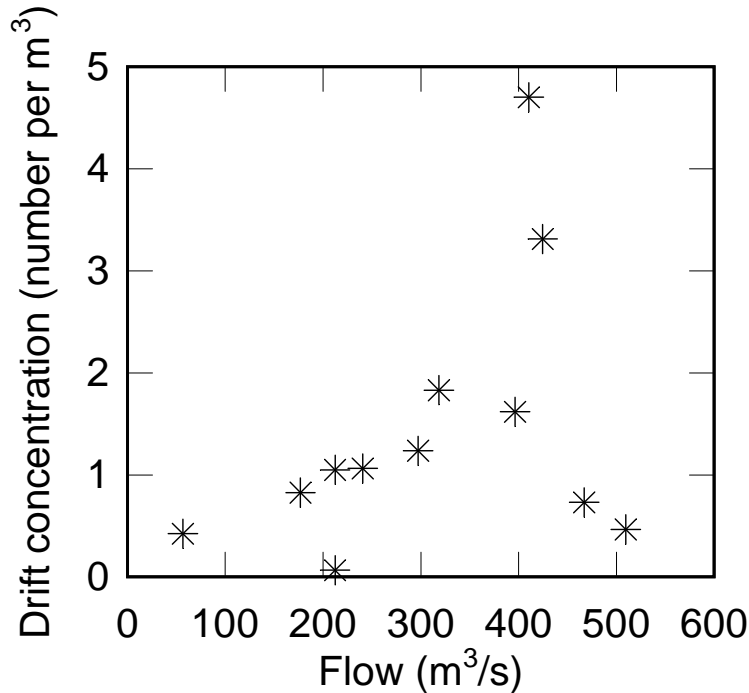
FIGURE 27 Drift Concentration Versus Flow during a Period of Fluctuating Flows Downstream of Glen Canyon Dam; from Tables 2 and 4 and Figures 3–14 of Leibfried and Blinn (1987). Each point represents one of six samples taken during a 24-h period, with one 24-h sampling period in each of three months. Drift concentration is the combined number of drifting *Gammarus* and chironomids. Flow is the approximate mean flow during the four-hour period represented by the drift sample.

The second hypothesized mechanism by which flow fluctuation could affect drift is by changing the overall production of drift. If flow pulses cause involuntary drift (invertebrates being unintentionally washed into the flow, whereas some invertebrates intentionally drift), the invertebrate source population (benthic or epifaunal) would be reduced. The question is whether such reductions in source populations would decrease or increase the overall rate of drift production. This question is analogous to "maximum sustained yield" management of fisheries. Low levels of harvest can increase a fishery's production by reducing the density dependence that limits production near the population's carrying capacity, while over-harvest can reduce production. If involuntary drift due to flow pulses corresponds to "harvest" of the source invertebrate population, moderate levels of flow-induced drift could result in higher overall drift production, while excessive levels of involuntary drift could reduce production.

There is no information regarding the effects of flow fluctuations on drift production at Flaming Gorge Dam. The Glen Canyon data collected by Leibfried and Blinn (1987) indicates that *Gammarus* drift concentrations were three times higher during three months of fluctuating flow than during the five-month period of stable flow; however, this difference was not statistically significant (one-way analysis of variance followed by Bonferroni *t*-test, $p=0.05$, six

samples for each month). Chironomid drift was slightly (but not significantly) lower during the fluctuating flow months. These results are not conclusive and could have been confounded by differences in season and mean flow between the two periods. However, the flow fluctuations clearly did not cause a major decrease in drift.

Flow fluctuations could also affect benthic invertebrate populations by causing invertebrates to change location or behavior to reduce their risk of being washed away (something that *Gammarus* appears to be particularly good at [Hughes 1970]) and by reducing the river width during off-peak flows. Figure 3 indicates that width changes due to load-following flow fluctuations are minor, except in dry years and especially at the Indian Crossing and Tailrace sites.

Two simulation analyses were conducted to address these two mechanisms by which flow fluctuations could affect drift. To address the first mechanism, simulations assumed that drift concentration increases with flow during within-day fluctuations. These simulations were identical to those of Experiment 1 (Section 3.1) except that hourly drift concentrations were adjusted by the hourly flow, assuming drift concentration is proportional to flow. For each hour, the daily mean drift concentration was multiplied by the ratio of the hourly flow to the daily mean flow. Under this scenario, the daily mean drift concentration therefore remains unchanged, but the total drift availability (biomass of food available to trout; equal to drift concentration times flow, summed over a day) increases with fluctuation magnitude because higher concentrations occur during higher flows (Figure 28). At 100% fluctuation, total drift volume is 72% higher than with steady flows.
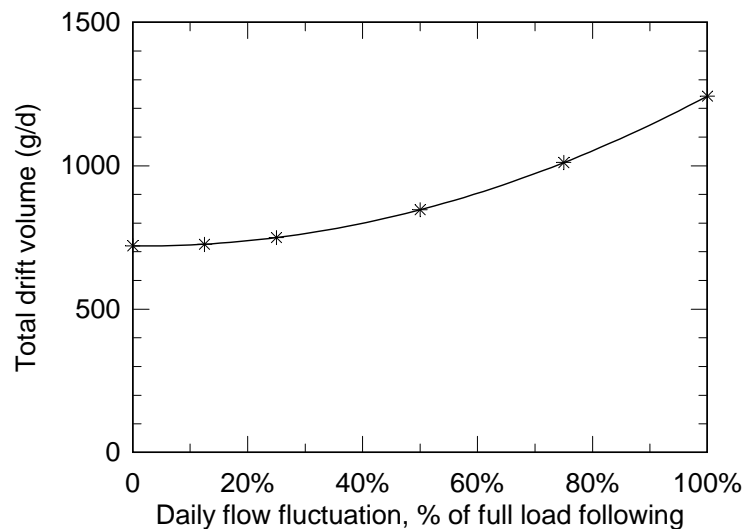
**FIGURE 28 Total Daily Volume of Drift (g/d) Passing
Any Transect, as a Function of Flow Fluctuation Magnitude,
in the Scenarios with Drift Concentration Proportional
to Hourly Flow**

The analysis for the second mechanism simply evaluates the trout population's sensitivity to drift concentration. Whether flow fluctuations increase or decrease, overall drift production is not known conclusively, but the importance of such effects can be evaluated. For this analysis, the simulations of Experiment 1 were repeated, but using four different drift concentration scenarios. These scenarios are 60%, 80%, 120%, and 140% of the baseline scenario drift concentration.

To make these experiments computationally feasible, they were conducted only for the Little Hole and Tailrace sites, and only for average hydrologic years.

5.2 RESULTS

5.2.1 Effects of Assuming Drift Increases with Flow

Would the relationship between trout population production and flow fluctuation magnitude differ if drift concentration varies with hourly flow rates? The simulation results (Figure 29 and Figure 30) indicate that it could. The effect is stronger at Little Hole (Figure 29), where production drops more steeply with fluctuation when drift is assumed to vary with flow. At both sites, however, production increases sharply at full load-following fluctuation levels for the scenario with drift increases with flow.
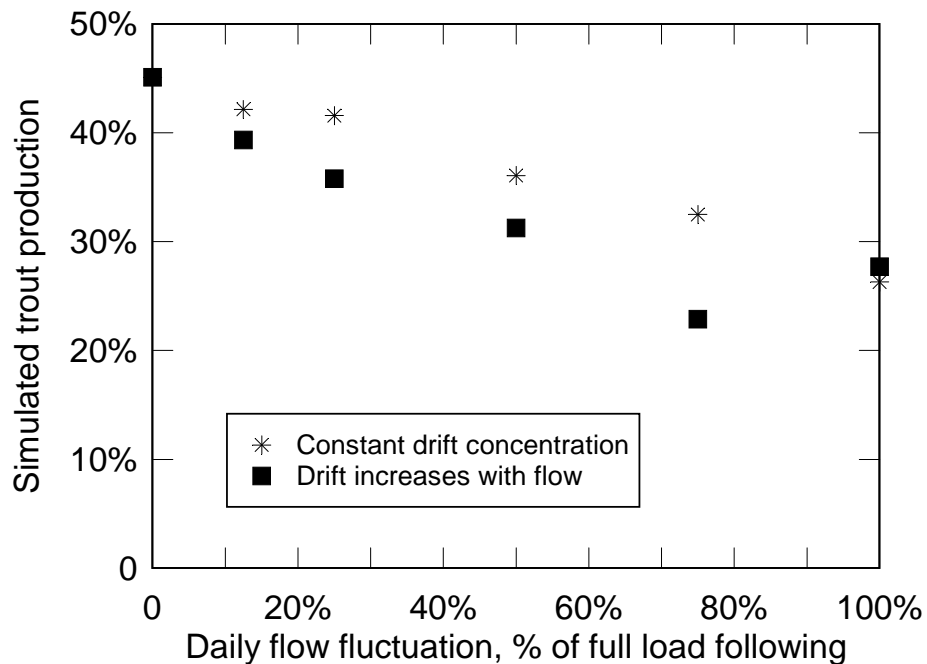
FIGURE 29 Comparison of Trout Production with Drift Concentrations That Are Constant vs. Flow-Proportional at the Little Hole Site in Average Years
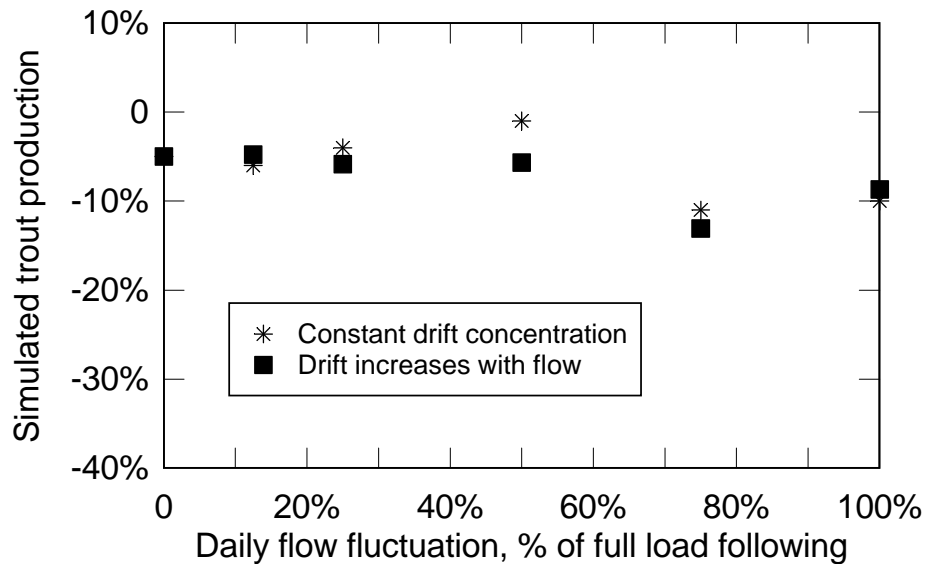
FIGURE 30 Comparison of Trout Production with Drift Concentrations That Are Constant vs. Flow-Proportional at the Tailrace Site in Average Years

It seems reasonable to expect that trout would feed more during on-peak flows in the scenarios with drift assumed to increase with flow. The simulated trout did so, especially at Little Hole (Figures 31 and 33). However, they also fed more during off-peak hours when drift varied with flow (Figures 32 and 34). Apparently, with drift reduced during off-peak hours, the trout responded by feeding more often (which also increases their exposure to predation).

5.2.2 Drift Sensitivity

This analysis examined how simulated trout production responded to uniform change in drift concentrations. Scenarios with drift concentrations 60, 80, 120, and 140% of the baseline values produced trout production predictably below and above the baseline production (Figures 35 and 36). In fact, for both sites the results of this analysis can be boiled down to a simple approximation: simulated trout production is proportional to the average drift concentration, with a proportionality constant of 0.75. For example, a 10% increase in drift produces a 7.5% increase in trout production, and a 20% decrease in drift produces a 15% decrease in trout production. A proportionality constant of 0.75 (instead of 1.0) indicates that the simulated trout partially compensate for changes in drift behaviorally: when drift increases, they reduce feeding somewhat to avoid risk, and when drift decreases, they increase the amount of time spend feeding to (at least partly) make up the lost growth.
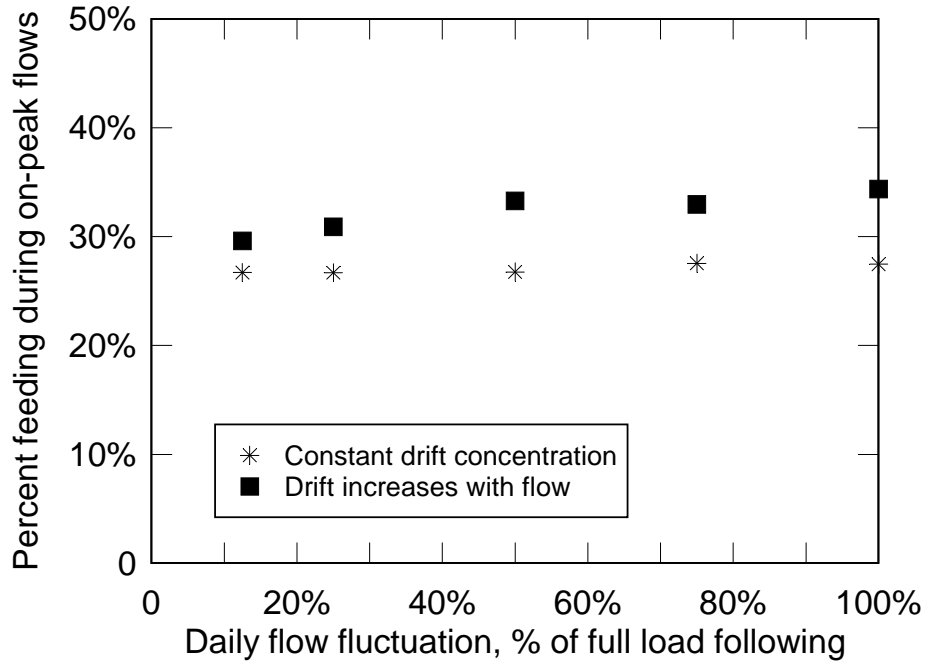
FIGURE 31 Mean Percent of Trout That Fed during On-Peak Flows at the Little Hole Site
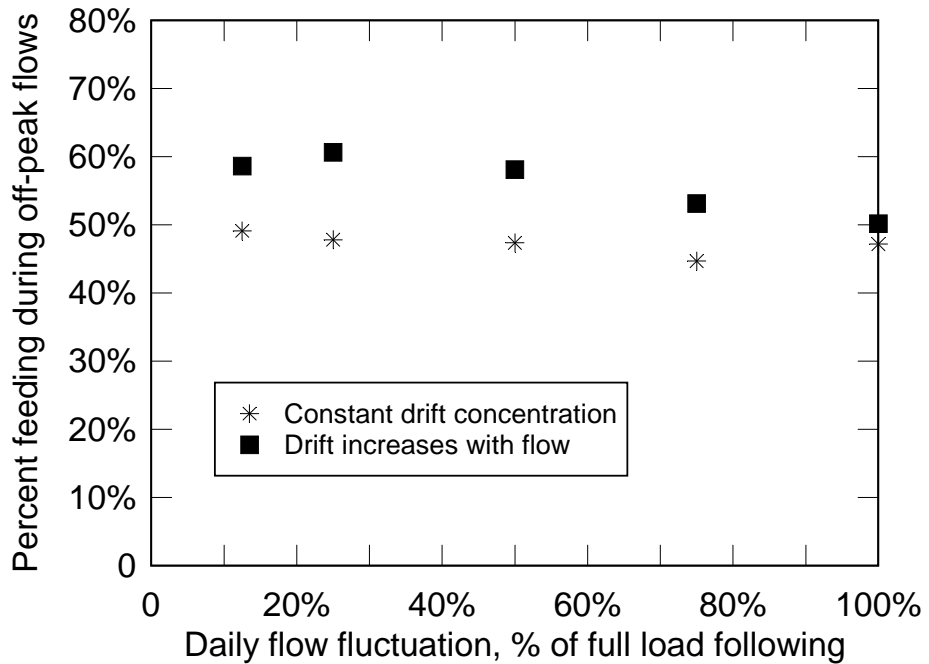
FIGURE 32 Mean Percent of Trout That Fed during Off-Peak Flows at the Little Hole Site
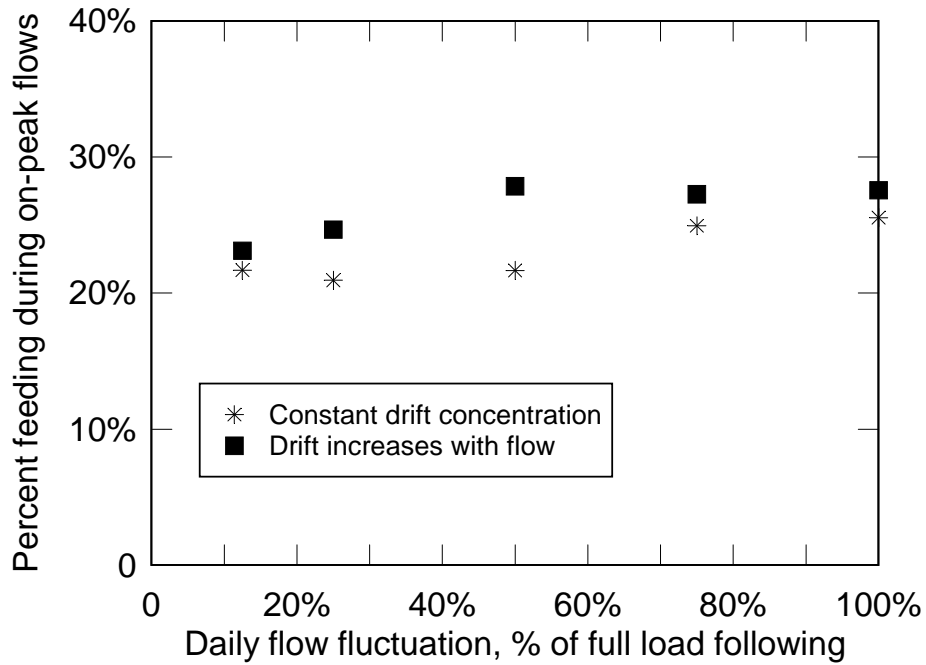
FIGURE 33 Mean Percent of Trout That Fed during On-Peak Flows at the Tailrace Site
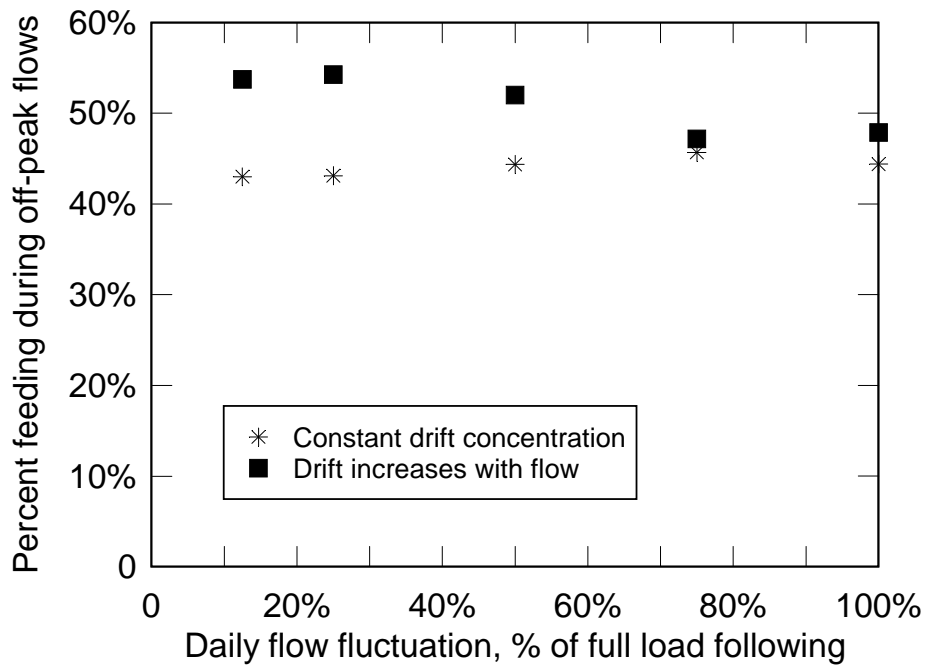
FIGURE 34 Mean Percent of Trout That Fed during Off-Peak Flows at the Tailrace Site
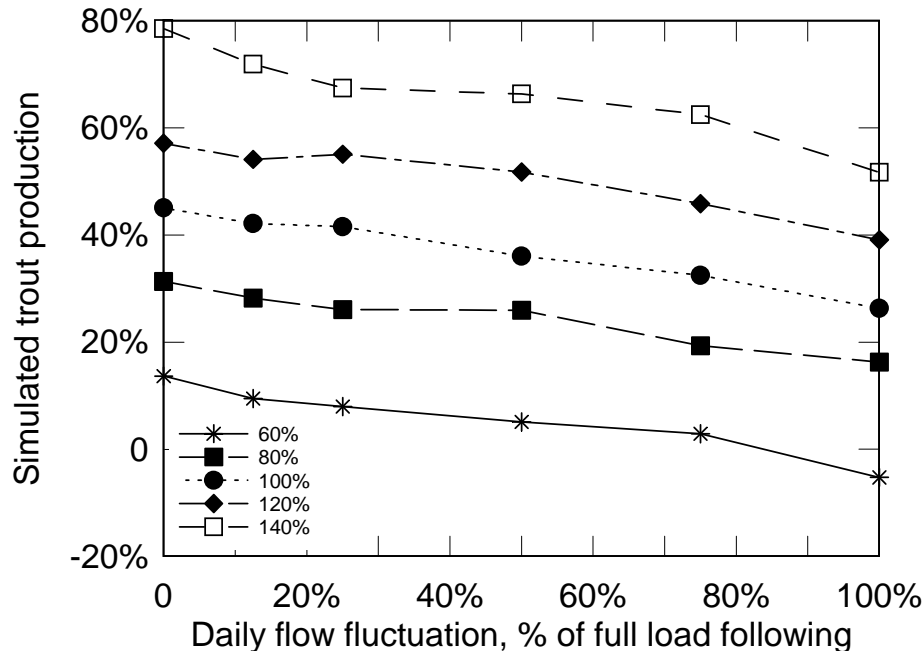
FIGURE 35 Sensitivity of Simulated Trout Production to Drift Concentration at the Little Hole Site in Average Years. Each line represents how simulated trout production varies with flow fluctuation magnitude, for one drift food concentration scenario. The drift scenarios range from 60 to 140% of the baseline value.

5.3 DISCUSSION FOR EXPERIMENT 3

The first analysis of this experiment indicated that the within-day timing of drift can interact with flow fluctuations in affecting trout production. If drift concentrations increase during flow pulses, as the very limited evidence from Glen Canyon Dam (Leibfried and Blinn 1987) indicates, the simulation analysis indicates that flow fluctuation effects may be more negative (at intermediate levels of fluctuation) than indicated in Experiment 1. However, this effect was not severe at Little Hole and very small and inconsistent at Tailrace.

The most likely explanation for these results is that, when drift is assumed proportional to flow while daily mean drift concentration is held constant, drift concentrations during off-peak flows decrease as fluctuation magnitude increases. During the average runoff year simulated here, flows are off-peak for 18 hours per day. Only at the highest fluctuation level does the increased total food availability (Figure 28) appear to offset the off-peak decrease in concentration.

The second analysis shows that overall drift concentration is predicted by *inSTREAM-SD* to strongly affect trout production, with changes in average drift concentration producing changes in trout production that are 75% as strong. However, the relationship between trout production and flow fluctuation magnitude was not affected by drift concentration. This analysis
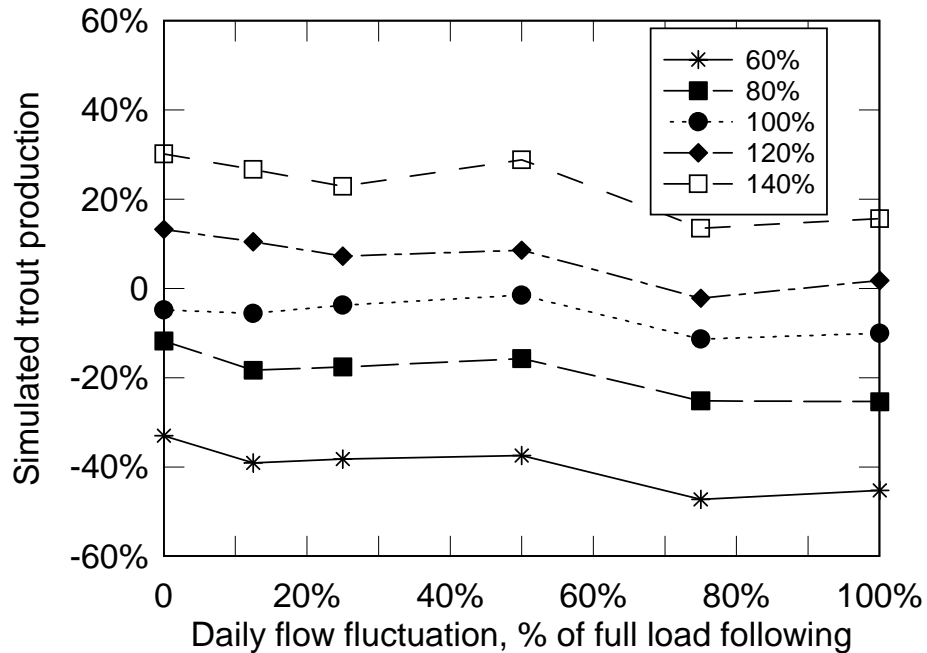
FIGURE 36 Sensitivity of Simulated Trout Production to Drift Concentration at the Tailrace Site in Average Years. Each line represents how simulated trout production varies with flow fluctuation magnitude, for one drift concentration scenario. The drift scenarios range from 60 to 140% of the baseline value.

provides confidence that the conclusions of all the experiments are not sensitive to how drift concentration was calibrated.

Another point very apparent from Figures 35 and 36 is that *inSTREAM-SD* predicts that trout production is much more sensitive to food availability than to flow fluctuations. In these figures, the change in trout production along each line (as fluctuation magnitude increases from 0 to 100%) is small compared to the change among lines as drift concentration changes. This result suggests that further research on flow fluctuation (or other management issues) could concentrate on effects on macroinvertebrates while assuming that trout populations will respond strongly to any changes in macroinvertebrate production.

6 SUMMARY AND CONCLUSIONS

This study addresses several key concerns about the effects of flow fluctuations from hydropower load-following on the trout fishery downstream of Flaming Gorge Dam. Effects of within-day flow fluctuations remain controversial and poorly understood, largely because of two problems: (1) fluctuation effects are virtually impossible to evaluate directly from field studies, and (2) effects depend (as this study indicates) on other factors such as study site and hydrologic year type. Computer simulation experiments with an individual-based trout model are a way to circumvent these problems. Simulation experiments allow us to control important variables and address natural variability. This study used simulation to address three research objectives that are key to management decisions at Flaming Gorge Dam but are not easily addressed using field research:

- How are trout populations affected by the magnitude of flow fluctuations? How does the difference between off-peak and on-peak flow affect trout production?

- Does releasing two flow peaks per day (double peaking) have greater effects on trout than releasing one peak?

- What is the potential effect of fluctuation-induced changes in the amount and timing of invertebrate drift on trout production? What if flow fluctuations change the overall drift rate or cause drift rates to vary with flow within the day?

This study used *inSTREAM-SD*, one of a family of individual-based river trout models developed by Lang, Railsback & Associates and Humboldt State University for Electric Power Research Institute, Inc. (EPRI), the U.S. Forest Service, the U.S. Environmental Protection Agency, and the Western Area Power Administration. For this study, *inSTREAM-SD* was developed to represent how sub-daily flow changes affect trout populations. This model represents a study site as a collection of rectangular cells, each with depth and velocity that vary with flow. The model represents each individual trout in the site's population. The virtual trout use well-tested algorithms to decide which habitat cell to occupy and whether to feed vs. hide; these decisions depend on the potential growth and mortality risks available in each cell, and are repeated each time the flow changes and each time night turns to day and day to night.

Four study sites were simulated, using habitat data collected during the 1980s for UDWR instream flow studies. Additional information on hiding and feeding cover needed by *inSTREAM-SD* was collected for this study. One limitation of this study is that the UDWR habitat data are very limited and probably do a poor job of representing the habitat diversity of each site.

A set of initial analyses examined how simulated trout production varies with flow in the absence of fluctuations. Results (from the upstream-most to downstream-most site) include:

- *Tailrace:* Trout production was low at flows below 32 m^3/s, then rose sharply to a flow of 35 m^3/s. Above this flow (which could be an artifact of the limited habitat data available at this site), production declined relatively steeply until flow reached around 60 m^3/s, after which it increased as flow continued to increase up to 130 m^3/s. Production at flows greater than 80 m^3/s was higher than the local peak at 35 m^3/s.

- *Pipe Creek:* Production rose steeply with flow to a peak at 50 m^3/s. Above 80 m^3/s, production rose again very gradually as flow further increased to 130 m^3/s.

- *Little Hole:* Production was low at 20 m^3/s and rose steeply to peak near 50 m^3/s, then decreased only slightly as flow further increased.

- *Indian Crossing:* Trout production was relatively insensitive to flow. Production peaked at 35 m^3/s but varied little between 20 and 70 m^3/s. Simulated production at Indian Crossing was substantially lower than at other sites as a result of its low availability of cover for feeding and hiding.

One of the clearest results of this study is that flow fluctuations are not predicted to have drastic effects on trout populations under any of the simulated conditions at Flaming Gorge Dam. Trout habitat is not severely reduced during either on- or off-peak flows. Neither is habitat for invertebrate food production, as indicated by wetted area. This result is specific to Flaming Gorge Dam and is in contrast to conclusions reached at some other hydropower projects (e.g., the Tallapoosa River study by Kinsolving and Bain 1993). One reason why load-following at Flaming Gorge Dam is not predicted to have severe effects is that the differences between on- and off-peak flows are less drastic than at some other projects. A second reason is undoubtedly that the Green River channel below Flaming Gorge Dam is relatively confined and U-shaped, so its wetted area does not change sharply with flow. (There is also no historic field evidence of flow fluctuations causing major declines in trout populations at Flaming Gorge.)

The simulation analysis of how the magnitude of daily flow fluctuations affect trout production indicates that fluctuations have generally small, usually negative effects. Effects vary among sites and among hydrologic year types; for example, low to medium fluctuations produced higher production than steady flows at Pipe Creek in wet years and at Tailrace in average years. The difference in annual trout production between no and full load-following was typically 5 to 15% of initial trout biomass, and always less than 20%.

Interruption of feeding is commonly cited as a mechanism by which flow fluctuations adversely affect trout: when flow changes, trout move in response and their feeding is disrupted when they move. This mechanism was simulated by assuming trout lose a quarter-hour of feeding if they choose to move and then resume feeding. The effect of this "feeding penalty" was a relatively small and uniform decrease in production; this mechanism appears to have little effect on the relationship between fluctuation magnitude and trout production. Even doubling the feeding penalty did not cause production to decrease more sharply as flow fluctuations increase.

One reason for this lack of effect is that trout move relatively often even in the absence of flow fluctuations, as they use different habitat for feeding vs. hiding and for daytime vs. nighttime feeding. A second explanation is that the effect of feeding disruption, as it was simulated, depends on the number of times a fish moves, not the distance it moves. The simulations indicate that the distance fish move among habitat cells increases with the magnitude of flow fluctuations, at least over low to medium fluctuations. If trout feeding really is disrupted significantly by moving, and the disruption increases with the distance moved, then the effects of flow fluctuations on trout production would be somewhat higher than indicated by this study.

An obvious and potentially important conclusion from the analysis of how fluctuations affect feeding and production is that slow, gradual changes in flow rate may be worse than rapid changes. If feeding is disrupted during flow changes, then the disruption would be minimized by minimizing the time during which flow is changing between off- and on-peak rates.

Double peaking—generating power with two shorter-duration daily peaks instead of one longer peak—was predicted to have a consistent but quite small (2% of initial trout biomass) negative effect on trout production. This effect is due to additional movement of trout in response to twice as many flow changes per day, so its magnitude depends on the assumptions for how moving affects feeding. Double peaking was predicted to cause more, but not twice as much, movement as single-peak operations.

Perhaps the most important insight resulting from the flow fluctuation experiments is a new way to understand and predict fluctuation effects. The simulated effects of flow fluctuations are dominated not by the "feeding penalty" concept but instead by the way fluctuations change the flow rate occurring during most of the day and whether that flow provides better or worse habitat for trout. For example, at the Tailrace site, trout production is predicted to increase as fluctuations increase in magnitude from 0 to 50% of full load-following, in average hydrologic years; but production decreases over this range in dry years (Figure 14). The explanation is found by looking at off-peak flows in average and dry years (Figures 8 and 9) and the relationship between base flow and trout production for Tailrace (Figure 6). Trout production at Tailrace peaks at a flow rate of 35 m^3/s. During average years, as fluctuation magnitude increases, the off-peak flow decreases from 50 m^3/s toward the peak at 35 m^3/s. However, in dry years, the off-peak flow decreases down from the peak value of 35 m^3/s as fluctuation magnitude increases.

Another way of stating this conclusion is that in scenarios—such as the dry and average years—when there are few on-peak hours, effects of flow fluctuations are dominated by how good the habitat is during off-peak flows. (During wet years when there are many on-peak hours, fluctuation effects are likely predictable from the average of habitat conditions over both on- and off-peak hours.) To confirm this conclusion, trout production is plotted in Figure 37 as a function of off-peak flow during dry and average scenarios (including results from both single- and double-peaking scenarios), along with results from steady flows (from Figure 6). These plots confirm that trout production in these fluctuation scenarios can be approximated fairly closely as the production resulting from steady flows equal to the off-peak flow. However, the more hours of on-peak flow there are per day, the less accurate this approximation will be.

This study also addressed indirect effects of flow fluctuations on trout via food production: fluctuations could affect production of the invertebrate drift that sustains the trout population. Not surprisingly, the drift simulations simply confirm that drift production is very important to trout production. The drift sensitivity experiment predicted that (at least over the simulated range of ±40% of baseline drift concentrations) for every 10% that drift concentration changes, there is a corresponding 7.5% change in trout production. In the simulation experiments, the effects on trout production of 10 to 20% changes in drift concentration were stronger than any of the effects of flow fluctuation. If flow fluctuations have strong effects on invertebrate production, trout could be more strongly affected by the changes in drift production than directly by the flow fluctuations.

Unfortunately, there is no conclusive evidence for if or how flow fluctuations affect drift production. The most relevant field study, from the Glen Canyon Dam tailwater (Leibfried and Blinn 1987), provides no clear conclusion but indicates that it is at least as likely that fluctuations increase overall drift production as it is that fluctuations decrease production. Ecologically, it is quite plausible that flow fluctuations increase involuntary drift at a rate that actually increases overall production, in the same way that sustained-yield harvest rates increase production of a fishery.
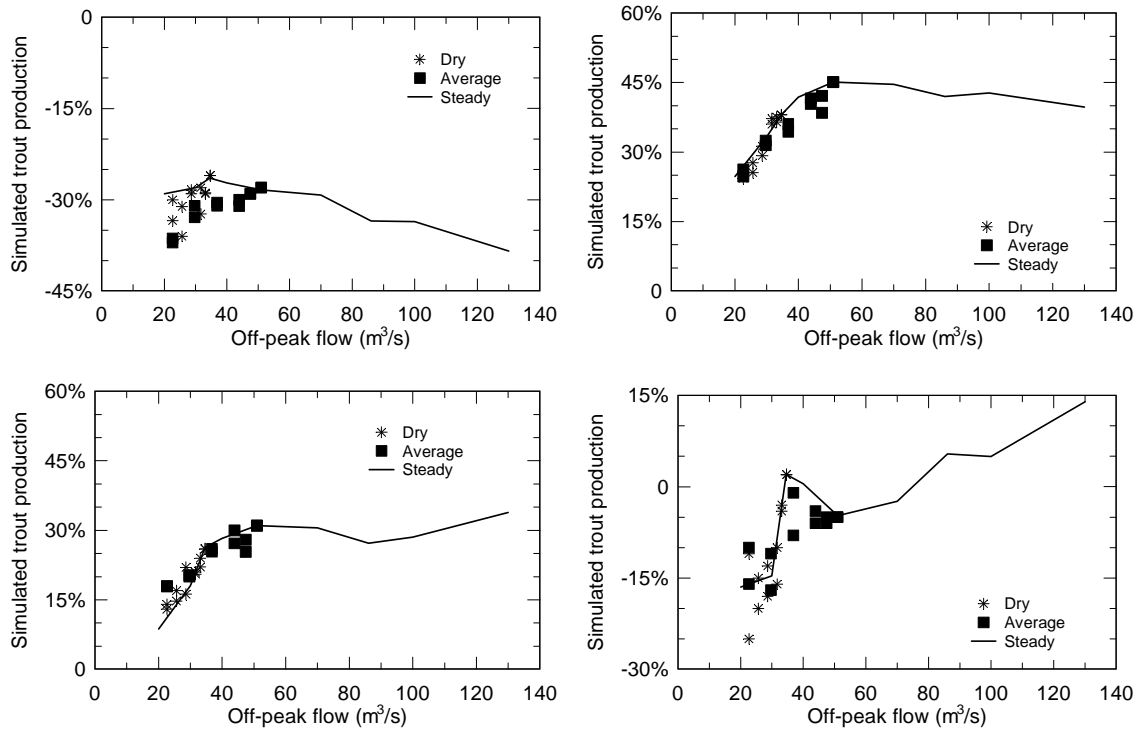
FIGURE 37 Simulated Trout Production vs. Off-Peak Flow for Dry, Average, and Steady Flow Scenarios. From left to right, top to bottom: Indian Crossing, Little Hole, Pipe Creek, and Tailrace sites, respectively.

Flow fluctuations have also been hypothesized to affect the timing of drift. The Glen Canyon Dam study (Leibfried and Blinn 1987) indicated that drift concentrations can increase during flow peaks. Assuming that drift concentrations increase in proportion to flow, and consequently are lower during off-peak flows, leads to increased effects of flow fluctuation magnitude on trout production. The increased drift during on-peak hours did not offset the reduced drift availability during off-peak hours. However, if instead it was assumed that drift is constant over base flows while increasing with on-peak flow, the result would likely be less of an effect of flow fluctuation on trout. There is no clear evidence for which assumptions are most realistic.

This study was subject to a number of uncertainties. The *inSTREAM-SD* model is complex and uses many assumptions and parameters. The most important assumptions about trout behavior (how they choose which habitat cell to occupy and when to feed vs. hide) have been shown in previous simulation experiments to reproduce a variety of patterns observed in field and laboratory studies, providing confidence in them. Simulation results undoubtedly depend on many of the parameter values, but no evidence was found that the model is unexpectedly or extremely sensitive to any parameters. The general conclusions drawn from the simulation experiments appear to be quite robust with respect to uncertainties in key parameters and inputs such as those controlling food availability and mortality risk. One of the most important uncertainties is the very limited data available from previous instream flow studies that model habitat at the study sites.

One benefit of simulation studies is that they can identify high-priority topics for future field research. In this study, there were two processes that stood out as (1) strongly affecting conclusions and (2) being particularly uncertain because there is little empirical research to support model assumptions. The first of these is how movement in response to changing flow affects feeding by trout. Do trout really cease, or reduce, feeding while moving in response to a flow change? Do they require time to find good habitat, establish dominance hierarchies or territories, and then resume feeding? Or do they simply continue to feed as they gradually adjust location as flow changes? Or can trout remember where good locations are at on- and off-peak flows and simply switch back and forth, as they sometimes switch back and forth between habitats for daytime and night feeding (Bunnell et al. 1998)? Methods for addressing these questions have been proposed (e.g., HSU 2004) but not implemented.

The second process identified as a research priority is how flow fluctuations affect production of drifting invertebrates at both the sub-daily time scale (does drift increase during flow peaks?) and in the long term. How long-term drift production varies with fluctuation frequency and magnitude is one of the most important questions for understanding how fluctuations affect trout, but we do not know with certainty whether flow fluctuations cause drift to increase or decrease (or, quite possibly, to peak at some intermediate fluctuation level). Unfortunately, relating drift to environmental conditions such as flow change can be expensive and challenging because drift is highly variable naturally and can be affected by factors other than flow (e.g., temperature). Changes in drift production are especially difficult to detect because fish eat the drift: an increase in the number of invertebrates entering the drift may not be detected by standard drift measurements because fish consume the additional food.

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APPENDIX A:

***inSTREAM-SD*: AN INDIVIDUAL-BASED TROUT MODEL APPLIED TO THE FLAMING GORGE TAILWATER, GREEN RIVER, UTAH**

APPENDIX A:

inSTREAM-SD: AN INDIVIDUAL-BASED TROUT MODEL APPLIED TO THE FLAMING GORGE TAILWATER, GREEN RIVER, UTAH

A.1 INTRODUCTION

A.1.1 REPORT OBJECTIVES

The primary purpose of this appendix is to document *inSTREAM-SD*, an individual-based stream trout model developed for research into the possible effects of alternative hydropower operations on the Flaming Gorge tailwater trout fishery. This model is one of a family of models referred to as *inSTREAM* (*in*dividual-based *S*tream *T*rout *R*esearch and *E*nvironmental *A*ssessment *M*odel), which have been developed, maintained, and researched by Lang, Railsback & Associates and Humboldt State University (see: http://www.humboldt.edu/~ecomodel). The *inSTREAM* models have been funded primarily by Electric Power Research Institute, Inc. (EPRI) and its member utilities, and also by the U.S. Forest Service and the U.S. Environmental Protection Agency. The most important difference between *inSTREAM-SD* and other *inSTREAM* models is that it represents sub-daily variations (thus, the SD designation) in flow and fish behavior.

The appendix has two main objectives. The first is to document how *inSTREAM-SD* was modified from its predecessor model (now referred to as *inSTREAM* Version 2) to adapt it to the Flaming Gorge site and study objectives. Version 2 of *inSTREAM* simulated trout in a relatively undisturbed, small mountain stream, and was designed primarily as a research model. It was fully documented by Railsback and Harvey (2001), which is available at http://www.humboldt.edu/~ecomodel/products.htm, and in a digital appendix to Railsback and Harvey (2002), available at http://www.esapubs.org/archive/ecol/E083/031/default.htm. This appendix does not fully document the Flaming Gorge model, but does fully document all of the changes made from the previous model.

The second objective is to document how the model was applied to the Flaming Gorge site. This documentation includes a description of model input and the analyses used to test and calibrate the model for analysis of Flaming Gorge management issues.

We have also published a journal article closely related to this report (Railsback et al. 2005). The article includes a summary description of the model, a description of the methods used to model how trout select a particular activity (feeding vs. hiding) and which cell to use each time step, and an analysis showing that the model reproduces a diversity of activity- and habitat-selection patterns observed in real salmonids. The analyses in the article provide an important validation, not documented here, of key assumptions of *inSTREAM-SD*.

A.1.2 FLAMING GORGE TROUT MODEL OBJECTIVES

The overall purpose of the Flaming Gorge trout model is to help understand and predict how reservoir and hydropower operations affect the tailwater trout fishery. Specific issues that the model is designed to address are:

- The effect of changes in reservoir release temperature on the production and downstream extent of the trout fishery.

- The effects of within-day flow variations on trout bioenergetics and production.

- Management questions such as how alternative stocking practices and harvest limits affect trout populations. (These management questions are not addressed in this report.)

A.1.3 STUDY SITE

The overall study reach is the tailwater of Flaming Gorge Dam, from the dam downstream to Taylor Flat. The model has been applied to four sites: (1) the Tailrace site, which begins just downstream of the dam and is 170 m long; (2) the Pipe Creek site, 482 m long; (3) the Little Hole site, 326 m long; and (4) the Indian Crossing Site just upstream of the Taylor Flat Bridge, 494 m long. We used habitat data from previous instream flow studies conducted at these sites.

A.1.4 CONVENTIONS

The following conventions are used throughout this document and in the model software.

A.1.4.1 Terminology

Definitions of terms used throughout this document:

Activity	The behavior a fish exhibits during a period. The activity is either *feeding* or *hiding*.
Day	The 24-hour calendar day that starts at midnight.
Daytime	The period of daylight, defined to start a specified time interval before sunrise and end a specified time interval after sunset (Section A.2.1.2).
Diel	A general term referring to differences between daytime and night.

Night   The period of darkness, starting a specified time interval after sunset and ending a specified interval before sunrise (Section A.2.1.2). One night includes parts of two calendar days, since it starts before midnight and ends after midnight.

Diel period   One daytime or nighttime. The "current period" means the day or night
(or "period")   period that starts at the current model time. "Following period" means the period of opposite phase that follows the current period. If it is the start of a daytime period at 06:00, the current period is the daytime that extends from 06:00 to 18:00 and the following period is the night period that starts at 18:00 of the current day.

Diel phase   Daytime or night. (The "current phase" is either "daytime" or "night.")
(or "phase")

Step   The time interval over which the model executes. This is equivalent to a typical model time step, except that the number of hours represented by each step is not constant (Section A.2.1.2).

A.1.4.2 Units

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

Most time-based parameters use day as the time unit. However, there are several exceptions to this convention. Flow and velocity variables are per second. All food intake, energy, and growth calculations use hourly rates because the number of hours per time step 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.

A.1.4.3 Parameter and Variable Names

To make 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 et al. 1999). 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").

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 followed for variables calculated by the model.

A.1.4.4 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, which is 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.

A.1.4.5 Dates, Days, Time, and Fish Ages

This model uses input in the "MM/DD/YYYY" format (e.g., 12/07/1999) for inputting dates. Hours are input as integers between 0 and 23 (although the 1–24-hour format is also acceptable in input files; hour 24 is converted to hour 0 of the following day upon input). The software converts this input to an internal date and time format that automatically accounts for leap years. All output uses the 0 to 23 hour convention.

Hourly data are assumed to be for local time; the model assumes that mid-day occurs at noon for calculating when day and nighttime periods end. The model assumes that hourly input always includes exactly 24 hours per day; there are assumed to be no days in the input containing 23 or 25 hours, due to changes between standard and daylight savings time. (Hourly input may or may not be generated using daylight savings time. The U.S. Geological Survey practice is to report hourly data using local time, which includes daylight savings time.)

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 each January 1.

A.1.4.6 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 habitat is mapped correctly by our software) and to correspond with terms used in popular instream flow models.

A.1.4.7 "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," which is a straight row of cells across the stream and floodplain perpendicular to the direction of flow. (The word "transect" is also commonly used to refer to a line across the channel along which depth and velocity are measured. We do not necessarily use this data collection approach, so we use "transect" to refer to a row of cells.) The number of habitat cells usable by fish varies with flow; e.g., cells on the stream margins may be dry at low flows.

A.1.4.8 X and Y Dimensions

The hydraulic model we use is one-dimensional, so our model represents the river as straight, and velocities have only one direction component: toward downstream. 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. The origin (X = 0) is at the downstream end of a reach, so water flows from right to left on an X-Y plot. The Y dimension is across the channel, or along a transect. 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.

A.1.4.9 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 cells.

A.1.4.10 Model Starting and Ending Times

The model user specifies the dates on which simulations start and end. By convention, the model always starts simulations on midnight (hour 0) at the start of the simulation start date and ends at hour 23 of the simulation end date.

A.2 MODEL DESCRIPTION: DIFFERENCES BETWEEN
inSTREAM-SD AND *inSTREAM* VERSION 2

This section documents changes made to the assumptions and equations used in the previous version of *inSTREAM*. Any parts of *inSTREAM-SD* not described here can be assumed to be documented accurately by Railsback and Harvey (2001). Likewise, any variables used but not defined in this section are defined by Railsback and Harvey (2001).

A.2.1 TIME STEP

Previous versions of *inSTREAM* use a one-day time step, using daily mean values for the driving habitat inputs (flow, temperature, turbidity) and executing fish methods once per day. This change implements a sub-daily time step, with driving variables updated hourly and fish methods executed a flexible number of times within each day.

A.2.1.1 Purpose and Assumptions

The previous versions of *inSTREAM* assume that flows are constant within a day, fish always feed during the day and not at night, and there is consequently no within-day movement. The purpose of allowing within-day movement is primarily to allow simulation of trout responses to within-day changes in flow, because within-day flow fluctuations are an important management issue for the Green River. This change also allows simulation of diel changes in habitat selection and behavior, which have been widely observed in trout.

The following fundamental assumptions underlie the new time step approach:

- Fish can select different habitats (change cells) for day vs. night. Diel changes in habitat result from diel changes in the growth potential and mortality risks in different habitats, not from diel changes in fish motivation.

- If flow changes significantly within a daytime or night period, the fish can choose new habitat in response. Such within-period movements are based on the same criteria and rules as the regular habitat selection at the start of each daytime and night period.

- Trout can remain active in both the daytime and night, if they choose to. Trout can also choose to be inactive during any period.

- The prediction of future survival probability that fish use to choose habitat considers diel differences in growth and risk. We assume the trout know that day and night both occur, and make their habitat choice considering their anticipated future day and night growth rates and survival probabilities.

- When trout choose habitat, they use a memory of feeding and risk conditions during the preceding diel period (daytime or night) as their prediction of conditions during the same phase on future days.

The assumptions are based on the following salmonid literature (see also Railsback et al. 2005): Young et al. (1997) found on average one-third of trout were active at night and 100% were active in day, in summer. Bremset (2000) showed that as temperature dropped at onset of winter, activity drops and fish gradually switch to nocturnal feeding; this paper also cites literature indicating that terrestrial predation risk is greater in winter because predators are active and fish cannot swim well to escape. Heggenes et al. (1999) also argued that predation risk is higher at low temperatures due to reduced swimming escape ability. Valdimarsson and Metcalfe (1999) and Jakober et al. (2000) showed that salmonids can feed at very low light levels, holding near the bottom and taking prey drifting above them. These two papers also document a shift to feeding in slower water at night. Heggenes et al. (1999) also provide literature on habitat shifts between day and night in summer, e.g., more use of slow, shallow habitat at night. Meyer and Gregory (2000) and Jakober et al. (2000) found that, in winter, adult trout were often concealed; more were concealed in day than in night, but during day and night, many fish were hiding. Small adults were found to use the substrate as hiding cover, whereas large adults used wood for cover.

Neil Metcalfe and colleagues at the University of Glasgow have conducted an extensive series of controlled laboratory and field experiments on diel activity and habitat selection in stream-dwelling juvenile Atlantic salmon and brown trout. Relevant results from this body of work include:

- As temperatures decrease, fish are less likely to feed during daytime (Fraser et al. 1995).

- In a laboratory situation, fish emerged from hiding cover for either very short or very long periods, supporting the assumption that the fish select one activity for an entire daytime or night period (Metcalfe et al. 1999). (However, Giroux et al. [2000] observed, in brown trout, frequent changes in activity within a diel period.)

- Diel activity patterns were found by Metcalfe et al. (1999) to vary with food availability.

- Fish occurred at higher densities in preferred habitat at night, compared to daytime (Valdimarsson and Metcalfe 2001).

- Diel activity pattern can be influenced by intraspecific competition, with less dominant fish displaced temporally from their preferred feeding period (Alanärä et al. 2001). A similar effect results from competition among species different in size (Harwood et al. 2001).

- Diel activity pattern can also be influenced by a salmonid's life history state; fish needing growth to advance to the next life stage (e.g., achieving reproductive maturity) may be more likely to use daytime feeding (Metcalfe et al. 1998).

- Daytime feeding is more common in fish that are in relatively low condition due to low food availability (Metcalfe and Steele 2001; an experiment conducted on minnows).

Several important conclusions are drawn from this literature; these conclusions include several observed patterns of diel habitat selection that were used to test the model by Railsback et al. (2005):

1. Diel differences in activity and habitat selection are widely observed in trout. Consequently, if we are going to model sub-daily changes in habitat, we need to consider the changes due to differences between daytime and night conditions. We should expect to see significant diel movement of trout even in the absence of flow changes.

2. The studies consistently show a pattern of the number of fish feeding at night instead of day increasing gradually as temperature decreases. Even in summer, there can be a significant fraction of fish that feed at night; when temperatures get <3°C or so (as they do at Flaming Gorge), almost all trout can be nocturnal.

3. Increased nocturnal feeding in winter is most often explained as a way to avoid predation risk. Trout are unable to swim as fast when it is extremely cold, so they are at greater risk to terrestrial, warm-blooded predators. Also, metabolic rates of fish are lower when temperatures are low, so they can get by with less food.

4. Salmonids are typically observed to use different habitat at night. Specifically, they use shallower and slower habitat where they are better able to see drift against the sky and catch it quickly. They appear to still be drift feeding, not searching the bottom. Feeding success appears to be a function of both the drift rate (which typically goes up at night) and light levels.

5. The habitat used by fish when hiding instead of feeding is not well defined because the hiding fish are very hard to find. They have been observed in woody debris and crevices among boulders.

6. The availability of hiding cover can be inadequate, so there can be competition for it, and some fish have been observed apparently unable to find hiding cover. In situations where hiding cover is limited (e.g., in the Green River below Red Creek, where the sand bottom provides little cover), it may

be necessary to explicitly model hiding cover to capture habitat selection dynamics.

A.2.1.2 Movement Triggers

To implement the diel and flow-based time steps, we define here (a) the criteria for delimiting trout movement time steps and (b) the kinds of model events that occur at particular time steps. The model checks conditions each hour and decides whether fish actions related to habitat selection should be conducted; other fish actions occur only once per day. This approach requires fewer computations than the alternative of simply using an hourly time step for all model events.

To implement our assumptions that fish move through the day and in response to changes in flow, we define two events that trigger fish movement (Table A.1). The first event is the switch between daytime and night. Daytime starts before sunrise and ends after sunset. The habitat parameter *habTwilightLength* is the number of hours that daytime is assumed to start before sunrise, and to extend after sunset. The variable *dayLength* is already included in the model; it is the calculated number of hours between sunrise and sunset. A new variable *numberOfDaylightHours* is therefore equal to *dayLength* + (2 × *habTwilightLength*). The second new variable *numberOfNightHours* equals 24 hours minus *numberOfDaylightHours*. Daytime therefore starts at a time (variable *daytimeStartTime*) equal to 12:00 minus (*numberOfDaylightHours*/2); and night starts at a time (variable *daytimeEndTime*) equal to 12:00 plus (*numberOfDaylightHours*/2). At the start of daytime and the start of nighttime, fish are allowed to move.

The second event that triggers fish movement is flow-based. If the river flow has changed since the last fish movement by a specified amount, then movement is triggered. The change in flow that triggers movement is equal to the flow at which movement last occurred (variable *flowAtLastMove*) times a habitat parameter *habFracFlowChangeForMovement*. If either of the following two conditions is met, then movement is triggered:

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

or

current flow < *flowAtLastMove* × (1 – *habFracFlowChangeForMovement*)

These criteria for delineating movement time steps are illustrated in Figure A.1, for an example period of fluctuating flows. In this example, the day length is 15 h and the value of *habTwilightLength* is 0.5 h, so movement triggered by the switch between day and night occurs at 04:00 and 20:00 each day. The other movements are triggered by flow changes exceeding a *habFracFlowChangeForMovement* value of 0.1. This value was chosen to allow fish to move whenever flow changed substantially.

Daylength = 15 Hours
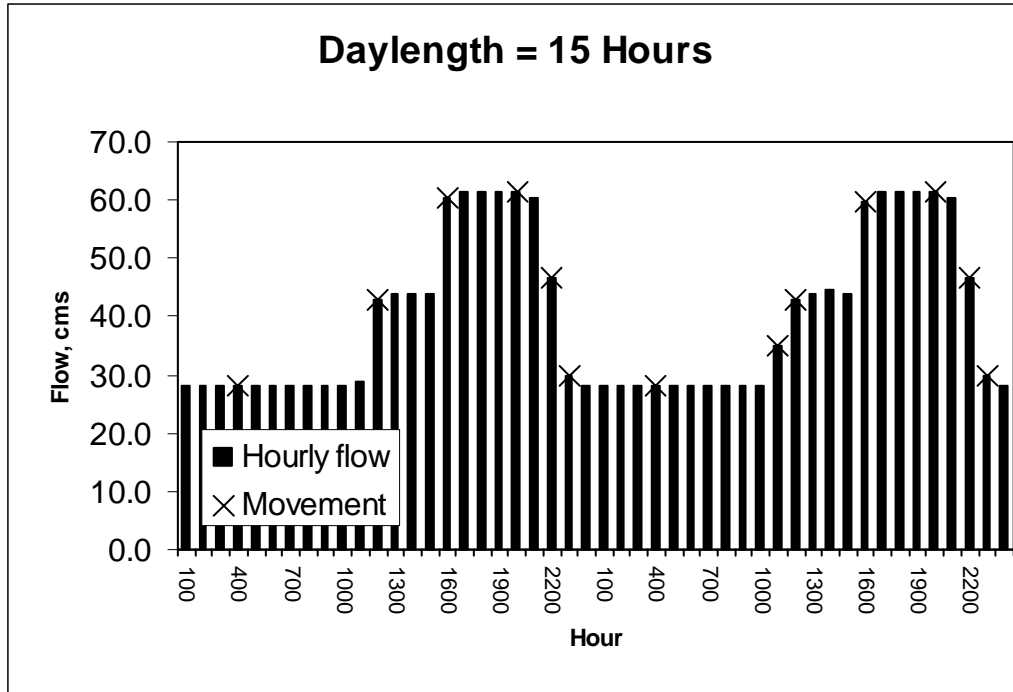
FIGURE A.1. Movement Triggers for Example Period of Fluctuating Flows. Each "×" indicates an hour at which fish movement is executed, because of either flow change or the switch between day and night.

TABLE A.1 Parameters Controlling Movement Time Step

Parameter	Meaning	Units	Value	Input File
habTwilightLength	Number of hours that daytime extends before sunrise or after sunset.	h	0.5	Habitat parameters
habFracFlowChangeForMovement	Fractional change in flow that triggers fish movement simulations.	None	0.1	Habitat parameters

A.2.1.3 Event Scheduling

The model executes events according to the following schedule:

Hourly events. For each hour simulated, the model reads the hourly flow from the input file and updates the model time (variable *currentTime*, h). The model uses the methods described above to determine whether a new time step was triggered by the new flow and time.

Time step events. If a time step is triggered, then the model conducts the following events in this order:

- Trout growth (simulating growth since the previous time step trigger, using the habitat conditions occurring since the previous trigger).

- Trout survival (simulating survival since the previous time step trigger, using the habitat conditions occurring since the previous trigger).

- Habitat update (cell variables are updated according to the flow, temperature, and turbidity for the current model time).

- Trout movement (allowing fish to move in response to the new habitat conditions).

Daily events. A number of events in the model occur at a daily time step. They are scheduled as follows:

- Daily maximum, minimum, and mean flow values are updated at midnight (hour 0), being calculated from the hourly flows for hours 0:00 to 23:00. The temperature and turbidity input are daily values, so these are updated at midnight. (This means that the daily flow, temperature, and turbidity used at midnight are the values for the following, not preceding, day.)

- Trout spawning (trout decide whether and where to spawn, then create redds) is scheduled on the first hour of daylight. Spawning is scheduled after growth and mortality in the preceding step are simulated, after habitat is updated for the new daytime period, and before movement is simulated. (Spawning is before movement, so the fish can move after they spawn.)

- Redd actions are scheduled on the first hour of daylight. These include redd survival, emergence, and development; and removal of empty redds. (Redd actions all use daily habitat variables.) Redd actions are scheduled after trout spawning, so new redds experience mortality and development on the day they were created.

- On the days when stocking of hatchery trout is simulated, stocking is arbitrarily assumed to occur at 10:00. Stocking is scheduled before fish

movement, allowing newly stocked fish to select their habitat before the next growth and mortality simulations.

- Fish ages are updated at midnight of January 1.

Observer events. When the graphical user interface (GUI) and output files are updated in relation to the model schedule affects the observed behavior of the model. In previous trout model versions, observer events all occurred at the end of each one-day time step. In this version, observer events are scheduled as follows:

- The GUI is updated every hour. On hours when a model step is not triggered, the GUI update only affects the display of model time and hourly flow rate.

- On hours when a model step is triggered, the GUI update occurs after all habitat, fish, and redd actions are complete. Therefore, the graphical display shows the model state after mortality and growth for the previous step are simulated, habitat is updated to reflect the flow rate for the new hour, and fish have moved in response to the new flow rate.

- On hours when a model step is triggered, the fish population status and mortality output files are updated after mortality simulations are conducted but before habitat is updated. Therefore, mortality output files reflect mortality occurring in the period between the previous step and the current one, and population output reports the status at the time the new step is started.

- Fish habitat selection output (the depth, velocity, etc., used by each fish; the number of fish in each cell) is written to file on hours when a model step is triggered, but is written after habitat is updated and fish movement is simulated. Therefore, the habitat selection output reflects the habitat and competitive conditions (number and size of other trout competing for resources) considered by the trout when they selected their habitat.

A.2.1.4 Habitat and Activity Selection Algorithm

Preceding versions of the trout model assumed that fish are active only in the daytime, so trout selected habitat to maximize Expected Reproductive Maturity (ERM; expected probability of surviving over a time horizon × expected fraction of reproductive size at the end of the time horizon) during daytime conditions. For *inSTREAM-SD*, we assume fish can be active daytime or nighttime, and select their daytime and nighttime habitat separately to maximize overall ERM. The value of ERM depends on survival probabilities and net energy intake over both daytime and night periods. We retain the assumption that fish evaluate ERM using the prediction that habitat conditions over the time horizon will be the same as current conditions.

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

- Feeding in the best cell during the daytime and hiding at night.

- Feeding in the best cell during daytime and feeding in the best cell at night (these cells could be different).

- Hiding during the daytime and feeding in the best cell at night.

- Hiding during both daytime and night.

There are many ways to model how fish evaluate these options. In designing *inSTREAM-SD*, we considered that these decisions could be made using an **optimization approach**, assuming fish:

1. Know the habitat conditions in each cell during the current period, including how much food is consumed by competitors (using the methods in the previous version of the trout model).

2. Predict habitat conditions in each cell during the following period. Habitat conditions can be predicted, e.g., by assuming they are the same as the current conditions except that the phase switches from daytime to night or night to day. To give fish a prediction of food competition, the model would have to track how many bigger fish have chosen to feed during the period, in which cells; this is similar to the previous trout model *except* that in the new model, fish are assumed to be able to predict competition in a future period instead of only in the current period.

3. Predict the survival probability and (negative) growth rate that would result from hiding during both phases.

4. Choose the optimal combination of daytime cell and activity (feeding or hiding) and night cell and activity that maximizes ERM, considering the total daily growth and survival probability. This optimal combination would not necessarily include the habitat cells that would maximize ERM, considering just daytime or night. For example, the optimal behavior in some cases may be to feed at night at a spot with relatively high mortality risk because it allows the fish to hide during the daytime; or to feed during the daytime in a cell with low intake and high survival, and feed again at night to maintain condition. The fish then moves to the cell chosen as optimal for the current period's phase (daytime or nighttime).

This optimization approach has three drawbacks. First, it would be computationally intensive because finding the optimal combination of daytime and nighttime habitat would

require evaluation of ERM for all possible combinations of cells. (Actually, the number of combinations to be fully evaluated can be substantially reduced by ignoring obviously inferior cells.) While this approach could noticeably increase execution times, it is not expected to be computationally infeasible. The second drawback is that we must give fish the ability to predict food competition levels in the following period. Previous versions of the model assumed fish know food competition in the current time period, knowledge that could be obtained through a few minutes of exploration. However, it is not clear what mechanism would allow a fish to know which competitors are where in a future period. Finally, the approach assumes a fairly high level of decision-making sophistication by the fish. This optimization problem is considerably more difficult than merely choosing the cell that provides the best current growth and survival conditions. The optimization approach may or may not be a good representation of actual fish habitat selection behaviors, but we consider alternatives that require fewer computations.

One way to simplify the habitat selection algorithm and eliminate questionable assumptions about the predictive ability of the fish is to constrain the optimization to a limited range of alternatives. We can, for example, greatly simplify the complicated optimization of daytime and nighttime growth and mortality risks by assuming fish do *not* predict growth and survival in all cells during the next upcoming period. Instead, we could assume that fish use a memory of growth and survival probabilities from the previous period as a prediction of growth and survival in the future period. The resulting **memory approach** would assume fish use these steps:

1. At the start of a daytime or night period, the fish knows the habitat and food competition conditions in each cell during that current period. From these conditions, it calculates the expected growth rate and survival probability it would experience if it either feeds or hides in each cell.

2. Fish retain a memory of the growth rate and survival probability they experienced during the preceding period. Furthermore, fish retain a memory of the growth and survival they predicted they would experience if they had chosen the activity (feeding vs. hiding) other than the one they actually conducted. For example, at the start of a night period following a day in which a fish chose to feed, the fish remembers (a) the actual growth rate and survival probability it experienced while feeding in the daytime, and (b) the growth rate and survival probability it predicted it would experience had it decided to hide instead of feed. The growth and survival during hiding were predicted by the fish during movement simulations at the start of the preceding daytime period.

3. Fish predict that the growth and survival probability they will experience in the following period will be equal to their memory from the previous period. For example, a fish deciding which habitat to select at the start of a daytime period predicts that during the following night it will be exposed to the growth rates and survival probabilities it remembers from the immediately preceding night period (for both feeding and hiding).

4. The fish chooses the cell and activity (feeding or hiding) for the current period that optimizes ERM, considering the predicted growth and survival for the hiding and feeding activities in the following period.

The memory approach's constrained optimization requires evaluation of ERM for only four alternatives for each of the potential destination cells, instead of requiring evaluation of all combinations of cells for daytime and nighttime periods. Only four alternatives require evaluation because the predicted growth and survival in the following period, for feeding and hiding, are fixed. The optimal cell (and hiding vs. feeding strategy) is the one that provides highest ERM for the best combination of:

- Feeding during the current period and feeding during the following period,

- Feeding during the current period and hiding during the following period,

- Hiding during the current period and feeding during the following period, or

- Hiding during the current period and hiding during the following period.

This approach eliminates the assumption that fish can predict food competition in the following period, but still assumes fish have the ability to trade off daytime vs. nighttime growth and survival rates to determine the best combination of daytime vs. nighttime activity.

A third approach is similar to the first optimization approach, but constrains the optimization by assuming fish do not make tradeoffs between daytime and nighttime periods; instead, fish determine the best cell for daytime-only feeding and the best cell for nighttime-only feeding, then decide which phase to feed in. In this **current period prediction approach**, each fish would conduct these steps at the start of each period:

- For each cell, the fish evaluates the ERM that would result if it (a) fed during the daytime (hiding at night), (b) fed at night (hiding during the daytime), or (c) hid during daytime and night.

- The fish identifies the best cell for each strategy: daytime-only feeding, night-only feeding, and all-day hiding, and calculates the ERM for conducting each of these strategies in the best cell. As with the optimization approach, this requires predicting food competition in the current and following period.

- The fish selects the strategy offering the best ERM, and moves accordingly. For example, if night-only feeding provides the highest ERM, and the current period is night, then the fish would move to the cell with the best night-only feeding ERM. If the fish determines that daytime-only feeding offers the highest ERM and the current period is night, then the fish hides in the cell with the best ERM for all-day hiding.

This approach eliminates one of the complex computations that the optimization approach assumes fish can make (trading off daytime vs. nighttime growth and survival rates to determine the best combination of daytime vs. nighttime activity) but retains another questionable assumption of the optimization approach, that fish can predict food competition in the following period.

A fourth approach does not depend on optimization but instead uses a simple heuristic to determine whether a fish should feed or hide each period. This **heuristic approach** assumes that a fish will choose to hide instead of feed only if it expects its condition factor (K, fraction of normal weight for its length) at the end of the period will remain above a threshold value (parameter *kForHiding*).

Using this approach, a fish would conduct these steps at the start of each period:

- Find the cell offering the highest ERM if the fish hides in it, under the current conditions. Determine what its K value is expected to be at the end of the period if it hides in this cell (*kExpectedIfHide*).

- If the value of *kExpectedIfHide* is greater than *kForHiding*, then the fish moves to the best hiding cell and hides there for the current period.

- Otherwise, the fish finds the cell offering the highest ERM for active feeding and moves there to feed for the current period.

In choosing a value of *kForHiding*, we must remember that this approach will cause fish to keep their condition very close to *kForHiding*. Therefore, its value should be only very slightly less than 1.0, because a condition of 1.0 represents the "normal" condition for a healthy fish. A value could be calibrated by finding the amount that K declines over periods when trout have been observed to hide instead of feed. The simplicity of this approach is appealing, but it does not provide fish with the ability to adapt their feeding behavior to such variables as mortality risk and seasonal changes in metabolism; analysis of previous model versions showed that such adaptive ability is essential for realistic simulation of habitat selection (Railsback and Harvey 2002).

Considering these four alternative approaches, we initially implement the second, the memory approach. A detailed formulation of the approach is in Section A.5.

A.2.1.5 Sub-daily Growth Simulation

With sub-daily time steps, trout growth is modeled each step. Modeling growth at each step is justified because (1) a trout's growth rate changes each step, (2) movement decisions at the start of one step can depend on the growth obtained during the previous step, and (3) the feeding and energetic methods that determine growth are appropriately simulated at hourly time scales. No changes in feeding and growth parameters are needed to use time steps as short as an hour.

The model was modified so that growth is calculated each step. At the start of each step, the growth occurring since the start of the previous step is determined, using the habitat and competitive conditions occurring during the previous step (Section A.2.1.3). The fish's size and condition are then updated before movement actions are conducted for the current step.

As part of implementing sub-daily growth, the model software was modified so that all food and energy intake, respiration, and net energy rates are hourly, instead of daily. Previously, some of these rates were calculated on a daily basis. However, there is one exception to hourly time steps: we continue to model the maximum food consumption (C_{max}, maximum grams of food consumed by a fish per day) at a daily time step. Maximum consumption is modeled at a daily instead of hourly time step because fish can fill their guts rapidly and then take many hours (especially at low temperatures) to digest the consumed food. This allows fish to obtain a full day's food consumption by feeding during only part of a day. We consider C_{max} in the fish's habitat and activity selection process in this way:

- When a fish calculates the expected fitness it would get from each combination of habitat cell and diel activity pattern (Section A.2.1.4), the food intake for each diel phase is not limited by C_{max}. The fish simply calculates how much food it could consume during day and night, limited by its feeding ability and food availability but not by C_{max}.

- The fish retains a memory variable *intakeForFeedingLastPhase* representing its food consumption (g/h) for the best food intake during the previous phase (the food intake for the best cell for feeding). This memory variable is maintained in the same way that the memory variable for net energy intake (*netEnergyForFeedingLastPhase*) is.

- The fish's memory variables representing the best food intake during the previous phase (*netEnergyForFeedingLastPhase* and *intakeForFeedingLastPhase*; Section A.5.1) are updated without being limited by C_{max}.

- When the fish calculates the fitness it expects for each diel activity pattern, it calculates the net energy it would obtain under each of the four possibilities (Section A.5.1). When this calculation is made, the fish checks whether its total food intake for a full day (the sum of *intakeForFeedingLastPhase* and the intake for the cell currently being considered) is less than or equal to C_{max}.

- If the full day's intake is greater than C_{max}, then the net energy intake for the full day is reduced to the level it would be if intake was equal to C_{max}. The total net energy is reduced by the amount (*total intake* – C_{max}) × *habPreyEnergyDensity*.

Actual food consumption is limited by C_{max} during the growth method in this way:

- The fish keep track of their total consumption in a full day. At the start of the daytime phase, the fish instance variable *fishActualDailyIntake* is set to zero.

- Fish have a variable (*fishFoodIntakeForBestCell*) for the food intake it would obtain in the best available cell, which is similar to the variable *netEnergyForBestCell; fishFoodIntakeForBestCell* is set to zero if the fish decides that hiding is the best behavior for the upcoming time step.

- The value of *fishActualDailyIntake* is incremented by *foodIntakeForBestCell*.

- If the value of fishActualDailyIntake exceeds C_{max}, then the net energy the trout obtains is reduced by the amount (*fishActualDailyIntake* – C_{max}) × *habPreyEnergyDensity*. Then *fishActualDailyIntake* is set equal to C_{max}.

However, the amount of food calculated as consumed by the model fish for the habitat cell is not adjusted for any limitations of C_{max}.

A.2.1.6 Sub-daily Survival Simulation

Mortality simulation uses daily survival probabilities that are a function of fish and habitat conditions. For example, a fish inhabiting a cell with a depth equal to 0.3 times the fish's length is estimated and modeled as having a 90% chance of surviving stranding mortality over one day. There are two challenges to simulating mortality at sub-daily steps. First, some survival probabilities may be timescale-dependent. Second, survival of fish must be simulated using daily survival probability values, when these probabilities vary among within-day steps.

Timescale-dependent survival probabilities. Survival probabilities are timescale-dependent if the survival probability is nonlinear with respect to the duration of exposure to risk. Predation risk is assumed to result from predator-prey encounters that occur over a few seconds or minutes, so the risk of being captured by a predator in two hours can be modeled as twice the risk of being captured in one hour and predation can be assumed *not* timescale-dependent. In contrast, the thermal stress risk to a trout exposed to a temperature of 26°C may be negligible over one hour, but very high over a full day (due to biochemical changes that become irreversible over several hours). Therefore, high temperature mortality is likely to be timescale-dependent.

The mortality risks included in the Green River model are: high velocity, stranding, poor condition, terrestrial predation, aquatic predation, and angling. None of these appear to be sufficiently timescale-dependent that the dependence needs to be considered in the model.

Simulating survival for each step. Survival of fish can be simulated either at the end of each sub-daily step using the survival probabilities occurring in that step, or at the end of a day using survival probabilities averaged over the steps occurring in the day. These two methods

would produce the same overall daily survival probability but different model results, because fish would die and be removed from the model at different times. Conducting the survival simulations each step requires more computations (requiring random numbers to be generated for each risk factor, each step) but allows the conditions under which the fish die (daytime vs. night) to be known. The averaging approach, on the other hand, does not allow the user to know the conditions which resulted in mortality, because survival is simulated only once for a day in which a fish was exposed to several habitat conditions.

We determine survival during each model step, instead of once per day. To adjust the daily survival probabilities for the step length, we simply raise the survival probability to the power (time step length [h] divided by 24 h).

A.2.2 DIEL VARIATION IN FEEDING

Darkness reduces the ability of fish to see and capture food, so we must assume feeding success differs between daytime and night. The previous trout model versions avoided this issue by assuming trout feed only during the day and the feeding formulation represented daytime conditions. Previous versions also forced the model to reproduce the observation that trout cease daytime feeding at low temperatures. Because we no longer restrict feeding to daytime, this section describes the changes made to the feeding model to represent differences between daytime and night. Our formulation is based on the literature reviewed in Section A.2.1.1.

Although the ability of fish to see and capture food is almost certainly a continuous function of light level, our model simply assumes two discrete light levels: daytime and night.

A.2.2.1 Drift Feeding

The primary variable driving drift feeding intake is the reactive distance—the distance over which we assume trout can see and capture food. Currently, reactive distance is modeled as a function of fish length, water velocity, temperature, and turbidity. Turbidity likely has an effect on reactive distance similar to that of darkness; turbidity reduces light levels but also reduces clarity.

At night, the lower light levels make food items more difficult to detect and more difficult to capture when detected. We use a constant factor, the input parameter *fishReactDistNightFactor* (unitless, with value between zero and one), to reduce the reactive distance at night. After reactive distance is calculated as a function of fish length and water velocity, temperature, and turbidity, it is multiplied by *fishReactDistNightFactor* if it is night.

The value of the *fishReactDistNightFactor* was determined from literature and tested during calibration (Section A.4.1). The relative ability of salmonids to see and capture food during daytime vs. night was studied by Fraser and Metcalfe (1997) and reviewed by Metcalfe et al. (1999). This literature does not provide a strong quantitative basis for modeling the effect of light level on feeding, but concluded that juvenile salmonids are, at light levels typical of

overcast to clear skies and a shaded stream, between 10 and 35% as efficient at capturing drifting prey as they are during the daytime. Schmidt and O'Brien (1982) measured reactive distance in Arctic grayling (another stream salmonid) feeding on large zooplankton at various light levels. Schmidt and O'Brien found that night reactive distances were 20 to 33% of daytime levels, but the zooplankton they used are smaller and more transparent than the macroinvertebrates that Green River trout mainly consume (Filbert and Hawkins 1995). This parameter could vary among sites due to factors like cloud cover and topography. It may be appropriate to use a value higher than these literature values, because skies in northern Utah are normally clear and prey are generally large.

We chose a value of 0.5 for *fishReactDistNightFactor*, which (because food intake varies approximately with the square of reactive distance) reduces feeding to 25% of daytime values. (Note that this formulation reduces the incentive for fish to use deeper water at night. The area of stream cross-section over which fish capture drift food is limited vertically by the minimum of the depth and the reactive distance; if the depth exceeds the reactive distance, there is no food intake benefit to using deeper water.)

A.2.2.2 Search Feeding

In the trout model, "search feeding" represents trout actively searching for stationary food on the stream bottom (or on the surface of still water). We assume that search feeding relies primarily on short-distance vision, but is also aided by tactile and olfactory senses. Consequently, we assume that search feeding is likely to be less successful at night, but not as affected by darkness as is drift feeding (which relies entirely on vision over longer distances).

We simply apply a constant factor, the input parameter *fishSearchNightFactor* (unitless, with value between zero and one), that reduces search feeding intake at night. After the search feeding intake (g/h) is calculated, it is multiplied by the value of *fishSearchNightFactor* if it is night. Using the same literature cited above for drift feeding, we selected a value of 0.5 for this parameter and then tested it during calibration (Section A.4.1).

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

A.2.2.3 Minimum Temperature for Feeding

In previous versions of the model, we used a parameter *fishMinFeedTemp* to defined the lowest temperature at which feeding occurs. This parameter forced the model to reproduce observations (e.g., Hill and Grossman 1993) that trout tend to stop feeding at low temperatures. Because the model now simulates diel variation in activity, it is no longer necessary or

appropriate to force fish to stop feeding at low temperatures; instead, changes in behavior with temperature and season should emerge. In observations of winter feeding, Bremset (2000) detected no lower limit on temperatures at which feeding occurs.

In *inSTREAM-SD*, we no longer use the parameter *fishMinFeedTemp* to force fish to stop feeding at low temperatures.

A.2.3 DIEL VARIATION IN SURVIVAL

This section describes how we model variation in survival probabilities between daytime and nighttime. We determined that aquatic and terrestrial predation and angling are the only mortality sources in the model that vary between daytime and night.

Given the trout model's overall complexity and the extreme difficulty of observing mortality risks (and the consequent lack of quantitative literature on the subject), we chose a very simple approach. We represent daytime and night as two discrete conditions, and assume that the base survival probability varies by a constant factor between these two phases.

We treat diel phase as a Boolean variable with two discrete values: daytime and nighttime. A more general approach would be to model survival probabilities (as well as feeding rate) as a continuous function of light level, and simulate how light level varies with time of day, season, and weather conditions. The light level approach has been used in models of how ocean fish migrate vertically in response to food intake and mortality rates that vary with visibility. The more general light level approach would also facilitate simulation of the effects of turbidity and depth (as well as phase of the moon and weather) on survival and feeding. However, the complexity of modeling light levels and how survival probabilities vary with light (which are likely to be highly nonlinear functions) seems not to be justified. Therefore, we assume survival probability changes discretely when the phase switches between daytime and nighttime.

We considered two approaches for representing the effect of night on predation survival: as a multiplier of survival and as another one of the "survival increase factors." The models for predation assume that survival probabilities vary with a number of habitat and fish variables, such as water depth and velocity and fish size. We treat the effects of each parameter separately, using "survival increase functions"; the variable with the highest survival increase function value determines the level of protection from predation. We could model the diel phase (daytime vs. nighttime) using another survival increase function that may or may not limit the predation survival probabilities. Using this survival increase function approach (for terrestrial predation), the predation protection provided by night would override the effects of other factors in most conditions, so, for example, depth would likely have no effect on predation risk. The second approach is to use separate minimum survival probability values for daytime and night—these are the base survival probabilities that are adjusted by the survival increase factors. This two-phase minimum survival approach assumes that the effect of night makes all habitats less risky (for terrestrial predation) and that the other habitat factors such as depth and velocity can still further reduce risk. The two-phase approach appears more realistic, while still being simple to implement, so we selected it.

The following two subsections describe how diel variation was added to the existing models for predation survival probability. The new angling survival formulation also includes diel variation, described in Section A.2.11.

A.2.3.1 Terrestrial Predation

Terrestrial predation survival is assumed to be much higher at night because most terrestrial predators depend on vision. Terrestrial predators that appear common at the Green River sites are birds (e.g., mergansers, ospreys, and kingfishers), otters, and shore-based mammals like raccoons and weasels. From a review of the literature addressing this issue, Metcalfe et al. (1999) concluded that otter and mink are primarily nocturnal predators, but that most predation is by birds, which are strictly daytime predators. Metcalfe et al. (1999) estimated that predation risk during foraging by river fish is 150 times greater during daytime than at night, in a system where 90% of mortality was due to birds, and fish were active and exposed to predation only 10% of the daytime and 90% of the nighttime. However, we estimate that in the Green River mammals cause a higher percent of the terrestrial predation mortality, and that on average a higher percent of trout are active in daytime, so that the difference between nighttime and daytime risks is lower.

We model diel variation in terrestrial predation using two separate values of the minimum survival probability used as a base value in the survival probability formulation (Table A.2). This parameter is the survival probability in the riskiest habitat, and the survival probability of a fish can be raised above this minimum by the survival increase factors that vary with fish size and habitat variables such as depth and velocity. Whereas previous versions of the trout model used a single parameter *mortFishTerrPredMin* to define minimum survival of terrestrial predation, we use two parameters: *mortFishTerrPredDayMin* and *mortFishTerrPredNightMin* to provide separate values for daytime and nighttime.

For the value of *mortFishTerrPredDayMin*, we initially use the value used by Railsback and Harvey (2001) for the Little Jones Creek study site, 0.99. We estimate that the mortality risk at night is 70% lower than in the day, so the initial value of *mortFishTerrPredNightMin* is 0.997. (The mortality risk equivalent to survival of 0.99 is 0.01; reducing the risk by 70% results in a mortality risk of 0.003, which is equivalent to a survival probability of 0.997). Version 2 of *inSTREAM* included a terrestrial predation survival increase function for day length. Because that version of the model assumed fish are active only during daytime, the risk of predation varies with the number of hours of daylight. The dependence of predation risk on daytime length is removed from the Green River model because daytime length effects are modeled explicitly.

We considered altering the terrestrial predation survival probability to assume lower survival during winter, a mechanism proposed by several authors as contributing to nocturnal feeding in winter (e.g., Fraser et al. 1993; Heggenes et al. 1999). At cold temperatures, fish cannot swim as rapidly and are less able to escape from warm-blooded terrestrial predators. However, this change was not made because important predators of Green River trout, especially mammals, are belive to exhibit lower activity levels in winter, and ospreys are absent in winter.

A.2.3.2 Aquatic Predation

We assume that survival of aquatic predation is lower at night: other conditions being constant, the risk of a juvenile trout being consumed by another fish is higher at night than during the day. Aquatic predation survival is modeled as lower at night for two reasons. First, bigger fish (predators) have bigger eyes and can see better than small fish at low light levels (Hester 1968, cited by Ware 1978). Second, larger fish, being released from terrestrial predation risk at night, tend to use shallower habitats where they are more likely to encounter small trout (Section A.2.1.1).

The dependence of aquatic predation survival on diel phase is modeled using two separate values of the minimum survival probability (Table A.2). We adopt a value of the daytime parameter *mortFishAqPredDayMin* calibrated at the Little Jones Creek site, 0.997. We estimate that mortality at night is 25% higher than during the daytime, so the value of *mortFishAqPredNightMin* is 0.996.

As with terrestrial predation, the dependence of aquatic predation on daytime length was removed from the model.

A.2.4 USE OF HIDING COVER

One consequence of modeling diel variation in trout activity is that we must consider what the trout do and what happens to them when they are not actively feeding. The studies cited in Section A.2.1.1 indicate that inactive trout are found in hiding cover, and that cover for hiding can be a limited resource that trout compete for. Hiding cover availability is a potential concern in the Green River where some sites (those like Indian Crossing that are below Red Creek)

TABLE A.2 Parameters for Diel Variation in Predation Survival

Parameter	Meaning	Units	Value	Input File
mortFishTerrPredDayMin	Minimum survival probability for terrestrial predation during daytime.	None	0.99	Fish parameters
mortFishTerrPredNightMin	Minimum survival probability for terrestrial predation during night.	None	0.997	Fish parameters
mortFishAqPredDayMin	Minimum survival probability for aquatic predation during daytime.	None	0.997	Fish parameters
mortFishAqPredNightMin	Minimum survival probability for aquatic predation during night.	None	0.996	Fish parameters

contain extensive sand deposits and little cover. Modeling use of hiding cover therefore requires representing the availability of cover, how it is allocated among trout, and how hiding cover affects survival probabilities.

A.2.4.1 Representation of Hiding Cover

To model the availability of hiding cover to individual trout, we adopt the simple approach already used to model the availability of velocity shelters for feeding. For each habitat cell, input data includes a value for the fraction of the cell having hiding cover (input variable *fracHidingCover*). We assume each fish that is in the cell and hiding instead of feeding uses up an area of cover equal to the square of the fish's length. Access to the available cover is given to fish in order of decreasing dominance—a trout cannot displace a more dominant trout from the available cover. (Dominance is equal to fish length multiplied by a species-specific weighting parameter, *fishSppDomFactor*.)

The area of hiding cover available in a cell is equal to the cell's area times its value of *fracHidingCover*. At the start of each time step, the area of hiding cover that remains available is set equal to *fracHidingCover*; any fish that decides to hide in the cell decreases the area of available cover by the square of its length. If the amount of cover available is less than the square of the fish's length, then the fish does not have access to hiding cover if it chooses to hide in the cell.

If no cover is available in a cell, remaining fish are not excluded from hiding in the cell. However, any additional fish that choose to hide there will have survival probabilities that do not include the benefits of hiding cover.

This approach is a highly simplified representation of hiding habitat. In reality, the availability of hiding cover varies with fish size (smaller fish being able to hide in some kinds of cover that are not available to larger fish), and hiding cover varies in quality. However, attempting to represent these processes adds complexity to the model that we do not feel is justified. (Van Winkle et al. [1996] attempted to simulate how the availability of cover varies with fish size.)

A.2.4.2 Effect of Hiding Cover on Survival Probabilities

Trout that are using hiding cover are assumed to have a higher probability of surviving three mortality sources: high velocity, terrestrial predation, and aquatic predation.

High velocity. High-velocity mortality represents exhaustion that would occur if a fish attempted to maintain itself in a cell having water velocity exceeding the fish's maximum sustainable swim speed. We assume that a trout using hiding cover in a cell with high water velocity would be sheltered from exhaustion, but still has some risk of being crushed or smothered by moving substrate. We assume that hiding cover decreases the risk of high-velocity mortality by 75% from the risk occurring if the fish swims at the cell's mean velocity. (The daily

survival probability is increased by an amount equal to 75% of the difference between no-hiding survival and 1.0; if the high-velocity survival is 0.8 without hiding, it is 0.95 with hiding cover.) This assumption is implemented by making high-velocity survival a "multi-function maximum" survival probability type, using the previous high-velocity survival function as the base probability and hiding cover as a survival increase factor. The new trout parameter *mortFishVelocityCoverFactor* (unitless; value = 0.75) is the fraction by which use of cover increases survival of high-velocity mortality.

Much of the hiding cover observed in the Green River is provided by aquatic vegetation (Section A.3.3.1). Vegetation of course provides less protection from high velocities than hiding in crevasses among rocks. However, hiding cover provided by aquatic vegetation typically occurs only in slow water; we assume that dense vegetation is unlikely to occur in cells where velocities are high. Very small trout can be affected by high-velocity mortality at relatively low cell velocities (well below 100 cm/s), and vegetation may well provide useful protection from such velocities.

Terrestrial predation. Observations have shown that use of hiding cover makes trout very difficult to find, even with electrofishing equipment (Section A.2.1.1), so cover use is expected to nearly eliminate the risk of terrestrial predation. We assume that use of hiding cover decreases the risk of terrestrial predation by 95%. In the terrestrial predation formulation, use of hiding cover is treated as a survival increase function, with the effects being independent of other factors that reduce predation risk. This is implemented by making use of hiding cover an additional survival increase factor for terrestrial predation. The new trout parameter *mortFishTerrPredCoverFactor* (unitless; value of 0.99) determines the amount that survival probability for terrestrial predation is increased if the fish is using hiding cover.

Aquatic predation. When hiding, small trout appear to use small spaces that protect them from larger, predatory trout. We model the effects of hiding cover on aquatic predation exactly as for terrestrial predation: use of hiding cover is a survival increase function that reduces mortality risk by 95%. The new parameter *mortFishAqPredCoverFactor* (unitless; value of 0.95) is used by this function.

A.2.4.3 Effect of Hiding on Swimming Speed and Respiration

We assume that fish that are hiding have negligible swimming speeds and activity respiration rates, whether or not they have access to hiding cover. This assumption is based on observations that trout not actively feeding typically find locations where they can avoid swimming, even if not hidden in cover in a cell with a positive average water velocity. The bioenergetics methods used to determine growth rates assume swimming speed is zero for any fish that is hiding.

A.2.5 FITNESS MEASURE FOR HABITAT AND FITNESS SELECTION

In previous versions of the trout IBM, fish rated alternative movement destinations using the "Expected Reproductive Maturity" fitness measure (Railsback et al. 1999). This fitness measure considers (1) expected survival over an upcoming time horizon and (2) for juveniles, how close to reproductive size they would be at the end of the time horizon. While this approach produced realistic behavior and growth in previous versions, it does not when we assume fish also choose whether to feed or hide each day and night—fish would choose to feed only enough to avoid starvation and hide the rest of the time, producing no growth. In reality, trout can grow to a large size in the Green River (>50 cm total length).

Instead, in this version of the IBM, we assume trout compare alternative decisions (combinations of habitat cell and activity) using a fitness measure that multiplies together (1) expected survival over the upcoming time horizon and (2) a function reflecting how fitness potential varies with the fish's expected length at the end of the time horizon. The "expected length" function models how expected fitness increases with the length the fish expects to attain by the end of the time horizon, which is a function of its growth rate.

The expected length function is justified by both empirical and theoretical considerations. First, some kind of function encouraging fish to continue growing once they reach the minimum reproductive size is required to reproduce the empirical observation that trout at the study sites grow much larger than the minimum for spawning in their species. These trout species spawn at lengths below 15 cm in some locations, yet grow to lengths above 50 cm in the Green River. Second, there are many fitness advantages to continued growth. Larger fish are better able to compete for better feeding and hiding locations. Maintaining high energy reserves reduces the risk of starvation during periods of poor growth conditions. Reproductive success (especially for females) also is likely to increase with size. Fecundity increases sharply with size; the IBM assumes an exponential increase in the number of eggs produced by a spawner as length increases. Larger females can bury their eggs deeper, reducing their risk of being scoured by high flows. Larger males can compete better for females. (There may be some fitness disadvantages to continued growth. Obviously, one is the additional risk of predation mortality assumed during feeding. Large fish need more food to avoid starvation, potentially making them more vulnerable during prolonged periods of poor growth. And large fish may not be able to hide as completely, or in as many sites, as smaller fish.)

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

survival. We do not expect, for example, that adult trout reduce their monthly survival probability by 5 to 10% in order to continue growing.

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

Considering these factors (and testing a variety of alternatives; Section A.4.3), we assumed an expected length function that is a logistic curve defined by two points: the function equals 0.7 at the minimize length needed for reproduction (the parameter *fishSpawnMinLength*) and equals 0.9 at the length of the largest fish currently in the population (Figure A.2). This function assumes that all fish "know" the size of the biggest fish in the population, which is inaccurate but a reasonable approximation. Each fish could only know the size of other nearby fish, but we expect the largest fish in the whole population to be a useful approximation of the largest fish that any individual must compete against. (This approximation is less accurate if there is a very small number of very large fish.)

The expected length function is not very sensitive to the length of the largest fish as long as the largest fish is sufficiently larger than *fishSpawnMinLength* (Figure A.2). However, as the largest fish's length decreases toward *fishSpawnMinLength*, the expected length function gets steeper for small fish and flatter for large fish. This means that the expected fitness of small fish increases more rapidly with size when the small fish are competing against smaller fish, but larger fish have less incentive to grow when they compete against smaller fish.

When the length of the largest fish gets too close to *fishSpawnMinLength*, the expected length function takes on undesirable characteristics, especially extreme steepness for small fish. Therefore, we limit the function by requiring its relative fitness (Y) value of 0.9 to be at a length at least 1.5 times *fishSpawnMinLength*. In other words, if the largest fish in the population is only 35 cm long and the value of *fishSpawnMinLength* is 25 cm, then the expected length function is defined to be 0.7 at 25 cm and 0.9 at 37.5 cm (1.5×25). (This function and its limit are hardcoded in the software, not controlled by parameters.)
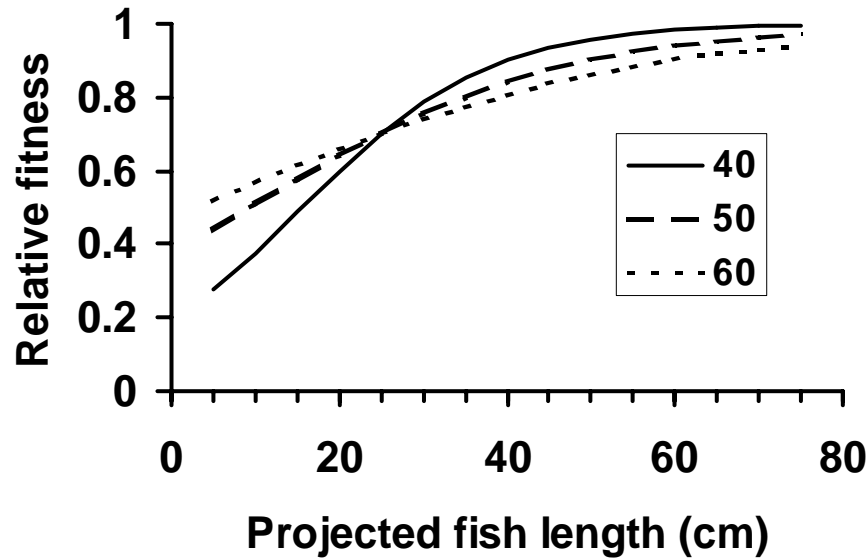
**FIGURE A.2 Expected Length Function for the Habitat and
Activity Selection Fitness Measure. The minimum spawning length
is 25 cm, and curves are shown for three values of the length of the
largest fish: 40, 50, and 60 cm.**

A second change in the fitness measure is in how growth over the future time horizon is
predicted. Other versions of *inSTREAM* predict growth over the time horizon by assuming a
constant absolute growth rate in grams of growth per day. For *inSTREAM-SD*, growth is
predicted by assuming a constant relative growth rate—the current relative growth rate
(*relativeGrowth*, grams of growth per day per gram of fish weight) is assumed to persist over the
time horizon. Hence, fish size at the end of the time horizon (*timeHorizon*, d) is calculated as
fishWeight × exp(*relativeGrowth* × *timeHorizon*).

A.2.6 FEEDING PENALTY FOR MOVEMENT

One of the mechanisms that have been suggested as determining the effect of rapid flow
variation on fish is that moving in response to flow changes disrupts feeding. To simulate this
mechanism, we added a penalty to food energy intake for fish that move. We assume that if a
fish moves to a different cell, it foregoes the amount of food it would have received during the
time period specified by parameter *fishMovePenaltyTime* (h). Furthermore, the fish is assumed to
swim at the cell's mean water velocity during the penalty time, without benefit of velocity shelter
(if the trout is drift-feeding) or hiding cover (if the trout is hiding). The total net energy intake for
a trout during a time step is equal to (1) the negative net energy intake during the penalty time
plus (2) the trout's hourly net energy intake rate for its cell and activity multiplied by (time step
length minus *fishMovePenaltyTime*). This penalty is imposed during the growth calculation for
the step following the move. This penalty is assumed *not* to be considered by the fish when

deciding whether to move; the alternative assumption that trout do consider the movement penalty would provide a small disincentive to movement.

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

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

A.2.7 MOVEMENT DISTANCE OUTPUT

The frequency and distance with which fish move are issues in assessing the effects of within-day flow fluctuations. The trout model can be used, for example, to simulate how the total distance moved by trout varies with the frequency or magnitude of flow changes. To allow such analyses, we added two trout variables that simply record and output the distance moved.

The new variable *fishDistanceLastMoved* (cm) is equal to the distance the trout moved the last time it executed its movement simulation. This distance is actually the horizontal, straight-line distance between the midpoint of the cell the fish started in and the midpoint of the cell it moved to. The variable *fishCumulativeDistanceMoved* (cm) is the cumulative distance moved by the trout over its lifetime; it is set to zero when the trout is created and is incremented by the value of *fishDistanceLastMoved* each time the fish executes its movement simulation. For output, we currently include the mean value of *fishDistanceLastMoved* (broken out by species and age) in a new output file called CumDistanceMoved.Rpt.

A.2.8 TEMPORAL VARIATION IN FOOD AVAILABILITY

It is well established that the drifting invertebrates eaten by trout typically occur at higher concentrations at night. Likewise, variation in drift concentrations (and the size and food value of drifting items) can vary with season and temperature. Given our formulations for habitat selection and feeding, such temporal variation in food availability could affect within-day and seasonal patterns of behavior and habitat selection and growth and survival rates. For example, in a field study of cutthroat trout in the Colorado River basin, Young et al. (1997) concluded that both diel variation in drift availability and light levels affect whether trout feed, but light levels were more important.

There are some measurements of diel and seasonal variation in insect drift below Flaming Gorge Dam. Filbert (1991, Filbert and Hawkins 1995) measured drift four times per year, at several times of day, at the Tailrace and Little Hole sites, finding major differences among seasons. (Incomplete sampling was also conducted at Browns Park.) Filbert and Hawkins (1995) also discussed drift in the Green River. However, these studies were of limited duration and are inadequate as a basis for predicting drift availability with any certainty.

To allow simulation of temporal variation in food availability, *inSTREAM-SD* treats the concentration of drift food (g/cm^3; previously the habitat parameter *habDriftConc*) as an hourly input variable. Users can therefore model drift concentration as a function of temperature, flow, etc., at hourly and longer time scales and input the resulting drift scenarios. Drift concentrations are read from a file, the name of which is specified in the Model.Setup file.

A.2.9 TROUT STOCKING

Large numbers of hatchery trout are stocked in the Flaming Gorge tailwater, and stocking is assumed to be a critically important source of recruitment for rainbow and cutthroat trout. Therefore, *inSTREAM-SD* was modified to simulate stocking.

A key assumption of the stocking method is that hatchery trout are identical in characteristics and behavior to other fish of their species. Hatchery fish have often been observed to display inappropriate behaviors (e.g., congregating in pools instead of searching out drift-feeding stations) and high mortality rates immediately after stocking. The model of Van Winkle et al. (1996) therefore treated stocked trout as a separate species with an inherently high mortality rate. Alternatively, hatchery fish could be represented as preferring stream habitat that resembles hatchery conditions until they learn appropriate habitat selection behavior (Railsback 2001). However, for the Green River tailwater, an initial high mortality of stocked trout does not seem sufficiently documented or important enough to justify inclusion in the model. Therefore, stocked trout are modeled from the start as identical to the other fish of their species.

A secondary assumption of the stocking method is that all stocked trout are initially in good condition and follow the same length-weight relationship used to define condition in other trout of the same species. The sizes of stocked trout are defined by their length distribution, and the model uses the same method to assign weights to newly stocked trout as is used to initialize the model's starting population.

The initial locations of stocked trout are randomly distributed throughout the modeled reach, except that no fish are placed in cells with depth less than 50 cm. Stocking is assumed to occur at 10:00 on the user-specified date. Stocked fish are assumed to feed instead of hide between the time they are stocked and the next time fish select their habitat/activity combination (Section A.2.1.2).

Stocking occurs in the model schedule before movement, so newly stocked trout are given the opportunity to move to better habitat before growth and mortality simulations are conducted. Under the model's rules defining the maximum distance a fish can move, a 15 cm stocked trout can move to cells within 45 m.

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

- Date of stocking (day, month, year),

- Species stocked,

- Number of trout stocked in the modeled reach,

- Age of stocked trout,

- Mean length of stocked trout, and

- Standard deviation of trout length.

The model uses this information to create the specified number and species of trout at the start of the specified day. The length of each individual fish is drawn randomly from a normal distribution with the specified mean and standard deviation. Any lengths that are less than half the specified mean are discarded, and a new length drawn. The weight of each fish is assigned from the length-weight relationship for healthy fish (see Sect. II.B, Fish Initialization, of Railsback and Harvey 2001).

A.2.10 HIGH TEMPERATURE MORTALITY: REMOVED

Previous versions of the trout model simulated potential mortality due to extremely high temperatures. Such temperatures (>24ºC) do not occur in the Flaming Gorge tailwater, so we removed this function from the model.

Note, however, that the Green River model still simulates important effects of high temperature. At high temperatures, metabolic rates are higher, so the same amount of food intake produces lower growth. As a consequence of lower growth, (1) starvation is more likely and (2) predation mortality can increase because trout may try to avoid starvation by using habitat with higher food intake but higher mortality risks. The model also still simulates high temperature mortality for trout eggs because this mortality occurs at temperatures as low as 16ºC.

A.2.11 ANGLING AND HOOKING MORTALITY

Angling is a common source of mortality in the Flaming Gorge tailwater but not included in previous versions of *inSTREAM*. The angler mortality model includes three separate components: fishing pressure, capture rate, and survival probability. Survival of angling is a function of whether a trout was caught, and the rate at which trout are caught is a function of fishing pressure. Hooking mortality (the subsequent death of fish caught and released by anglers) is modeled as a separate but related mortality source.

The fundamental assumption of the angler mortality formulation is that the risk to an individual fish of being hooked by anglers is a function of fishing pressure and not directly a function of trout abundance. The model assumes that anglers catch a constant fraction of the

catchable population, so if there are more fish, more are caught. However, the method for predicting fishing pressure includes a term for trout abundance, so abundance has an indirect effect on the risk per trout by changing the fishing pressure. The model also assumes that an individual trout can be caught more than once in a day, which seems not unlikely in the heavily fished Flaming Gorge tailwater.

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

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

We currently model fishing pressure using a set of 12 habitat parameters (*habAnglePressJan–habAnglePressDec*) that provide the value of *anglerPressure* for each month. Different parameter sets can be used to represent how fishing effort varies among sites. (These parameter values have not yet been fit to observed angler use rates.)

We also assume fishing pressure is lower at night than during the day. The nighttime reduction in risk is represented by the habitat parameter *habAnglePressNightFactor* (unitless), which is the fraction by which fishing pressure is reduced at night. Because night fishing is believed to be minimal at Flaming Gorge, we use a value of zero for this parameter for most sites. However, there are anglers that consistently fish at night below the Little Hole boat ramp; study sites in that vicinity could have a *habAnglePressNightFactor* value of 0.05–0.1 (personal communication, Gary Burton, Western Area Power Administration, email to John Hayse and Steve Railsback, July 13, 2001).

Capture rate is represented as the average number of times a fish is hooked per day. This capture rate is assumed to be a linear function of fishing pressure, with the proportionality constant being an input parameter (*mortFishAngleSuccess*) that represents fishing success as the fraction of catchable fish hooked per angler-hour. This parameter can vary among species to reflect differences in vulnerability to angler harvest. Capture rate is also assumed to be a logistic function of trout size. The size dependency reflects the success of anglers in selecting for larger trout by (a) using tackle more attractive to larger fish and (b) placing casts in spots that are better habitat for large trout.

The capture probability model is:

$$captureRate = mortFishAngleSuccess \times anglePressure \times reachLength \times 10^{-5}$$
$$\times \text{logistic}\,(fishLength)$$

where:

- *captureRate (*fish caught per catchable fish per day) has units of d^{-1},

- *mortFishAngleSuccess* (fish caught per catchable fish per angler-hr) has units of (angler-h)$^{-1}$,

- *anglePressure* has units of angler-h $\times$ km^{-1} $\times$ d^{-1},

- r*eachLength* is the length of the modeled reach in cm (all habitat distances are stored in cm),

- The factor 10^{-5} converts reach length in cm to km, and

- The logistic function of fish length (Figure A.3) is defined by the two trout parameters *mortFishAngleL1* and *mortFishAngleL9*.

Multiplying the parameter *mortFishAngleSuccess* by the number of catchable trout in a reach gives the expected number of fish caught per angler-hour, a common measure of angler success. Therefore, this parameter can be estimated and validated if the abundance of catchable trout and angling success are known for the same time period. In conducting such an analysis, the definition of "catchable" trout should be compatible with the logistic function used in the capture rate equation. Prior to fitting this parameter value, we use a temporary value of 0.01.

Note that this capture rate formulation does not include a saturation function for trout density—the probability of any individual trout being hooked does not decrease as the number of trout at a site increases. In reality, when trout are very dense and fishing success high, the fishing effort per angler could be limited by the time required to handle and release hooked fish.
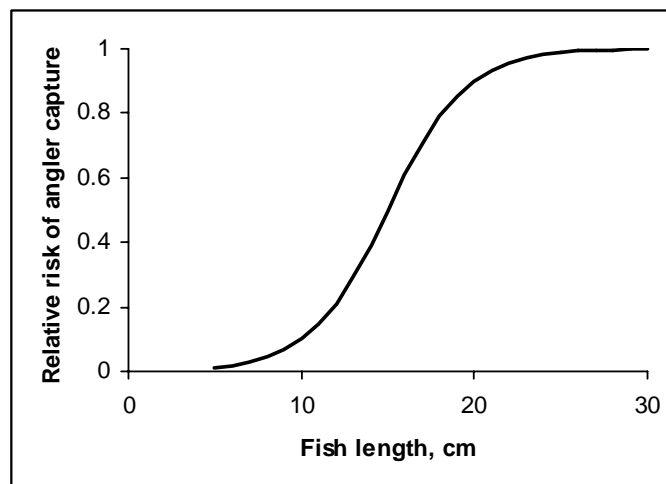
FIGURE A.3 Fish Length Function for Angler Mortality Probability of Capture

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

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

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

The Utah fishing regulations currently include a "slot limit": it is legal to keep trout that are less than 33 cm long or greater than 51 cm long. Separate probabilities of keeping hooked fish are applied to fish that are and are not within the legal length ranges. The slot limit is defined by two parameters: *mortFishAngleSlotLower* and *mortFishAngleSlotUpper*.

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

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

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

In summary, the following steps are used for each trout to determine the probability of surviving angler harvest (parameter values are summarized in Table A.3). The fishing pressure is updated at the start of each day, being constant within a day and among all habitat cells.

1. The daily capture rate is calculated from the fishing pressure and the trout's length.

2. A random draw from a Poisson distribution defined by the capture rate determines the number of times the fish is hooked during the time step (*timesHooked*). If *timesHooked* is zero, the survival probability is 1.0 for angling and hooking mortality.

3. If *timesHooked* is one or more, the slot limit parameters and fish length are used to determine if the trout is of legal length to keep.

4. Steps 5 and 6 are conducted once for each time the trout is hooked.

5. If the trout is of legal size to keep, a random draw is applied to the parameter *mortFishAngleFracKeptLegal* to determine whether the trout is kept. If the trout is not of legal size, a random draw and the parameter *mortFishAngleFracKeptIllegal* determine whether the trout is kept. If the trout is kept, the survival probability is 0.0.

6. If the trout is released (not kept), the survival probability for angling is 1.0, but the fish is tagged with the value of *timesHooked*. The trout is then subject to the hooking mortality source.

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

TABLE A.3 Parameter Values for Angler and Hooking Mortality

Parameter	Definition	Units	Value
mortFishAngleSuccess	Multiplier to determine capture probability from fishing pressure. May vary among species.	(angler-h)$^{-1}$	0.01
habAngleNightFactor	Factor (0–1) by which fishing pressure is reduced during night.	None	0.0
habAnglePressJan	Value of *anglePressure* for January.	angler-h d^{-1} km^{-1}	2
habAnglePressFeb	Value of *anglePressure* for February.	angler-h d^{-1} km^{-1}	2
habAnglePressMar	Value of *anglePressure* for March.	angler-h d^{-1} km^{-1}	5
habAnglePressApr	Value of *anglePressure* for April.	angler-h d^{-1} km^{-1}	10
habAnglePressMay	Value of *anglePressure* for May.	angler-h d^{-1} km^{-1}	25
habAnglePressJun	Value of *anglePressure* for June.	angler-h d^{-1} km^{-1}	75
habAnglePressJul	Value of *anglePressure* for July.	angler-h d^{-1} km^{-1}	100
habAnglePressAug	Value of *anglePressure* for August.	angler-h d^{-1} km^{-1}	100
habAnglePressSep	Value of *anglePressure* for September.	angler-h d^{-1} km^{-1}	75
habAnglePressOct	Value of *anglePressure* for October.	angler-h d^{-1} km^{-1}	50
habAnglePressNov	Value of *anglePressure* for November.	angler-h d^{-1} km^{-1}	10
habAnglePressDec	Value of *anglePressure* for December.	angler-h d^{-1} km^{-1}	5
mortFishAngleL1	Fish length at which relative risk of being hooked is 10% of maximum.	cm	10
mortFishAngleL9	Length at which hooking risk is 90% of maximum.	cm	20
mortFishAngleSlot-Lower	Length defining the lower end of the range in which fish are illegal to keep.	cm	33
mortFishAngleSlot-Upper	The upper end of the range in which fish are illegal to keep.	cm	51
mortFishAngleFrac-KeptLegal	Fraction of fish of legal length that are kept by anglers.	None	0.2
mortFishAngleFrac-KeptIllegal	Fraction of fish not of legal length that are kept by anglers.	None	0.05
mortFishAngleHook-SurvRate	Fraction of released trout (or trout that shake the hook) that survive.	None	0.8

A.2.12 AQUATIC PREDATION: PREDATOR DENSITY FACTOR

One of the "survival increase factors" that determine the survival probability due to aquatic predation (cannibalism by large trout) is the density of predator trout. In Version 2 of the trout model, predator density was evaluated as the number of trout age 2 or older per cm of stream length. This approach is less appropriate for the Green River, where there is less of a

relationship between trout age and size, due to rapid growth rates and stocking of hatchery trout that are large for their age. Whether a trout is piscivorous is generally considered to be a function of its size and species; larger trout are better able to catch and eat fish prey, and some species (e.g., brown trout) are believed to be more piscivorous. In this version of the model, we simulate whether fish are actively feeding vs. hiding, and only feeding fish should be considered predators.

We changed the aquatic predation function so that predator density is evaluated as the number of active (not hiding; Section A.2.1.1) piscivorous trout per square cm of stream area. Trout are defined to be piscivorous if their length exceeds a new trout parameter: *fishPiscivoryLength* (cm). Different values of *fishPiscivoryLength* are used as a simple way to reflect differences among species in piscivorous tendencies.

At the start of movement simulations for a model time step, the number of piscivorous fish (model variable *numPiscivorousFish*) is reset to zero. As each trout conducts its movement decision simulations and decides whether to actively feed or hide, the value of *numPiscivorousFish* is incremented for each fish that (1) has length greater than its value of *fishPiscivoryLength* and (2) decides to actively feed. Because fish simulate movement in order of descending dominance (which is mainly determined by length), this approach means that, during movement simulations, trout consider as predators only fish with greater dominance than themselves. This assumption is reasonable because all piscivorous fish should be included in *numPiscivorousFish* by the time fish small enough to be vulnerable to aquatic predation are processed. The final value of *numPiscivorousFish* (after all trout simulate movement) is retained and used when the survival simulations are conducted.

Some field observations are relevant to the value of *fishPiscivoryLength*. Diet studies (examination of gut contents of trout caught between 8 and 10 p.m.) in the Green River indicate that (1) very few trout had eaten other fish, and (2) all fish that contained other fish were brown trout with length greater than 30 cm (personal communication, Mark Vinson, Utah State University; email to John Hayse, June 18, 2001). These observations indicate that the high availability of invertebrate food in the Flaming Gorge tailwater may make piscivory less common than at other sites. (At the Little Jones Creek site used for Version 2 of *inSTREAM*, piscivory has been observed in cutthroat trout with length in the range of 15 cm.) To reflect the observed piscivory of brown trout and lack of piscivory in other species, *fishPiscivoryLength* is given a value of 25 cm for brown trout and a value of 40 cm for other species.

The density of piscivorous fish (habitat variable *piscivorousFishDensity*) is calculated by dividing the current value of *numPiscivorousFish* by the current area of stream habitat. The current area of stream habitat is calculated by summing the area of all cells with depth greater than zero at the current flow.

The trout parameters *mortFishAqPredP1* and *mortFishAqPredP9* (for the effect of predator density) are no longer used. Instead, we define the new parameters *mortFishAqPredA1* and *mortFishAqPredA9* to model how the number of active piscivorous trout affects aquatic predation survival. Parameter *mortFishAqPredA1* (piscivorous fish per cm^2) is the predator density at which survival is increased by only 10% above the minimum; we assume a value

of 5×10^{-6} (or five predators in a 10×10 m^2 of habitat) for this parameter. For *mortFishAqPredA9*, the predator density at which survival is increased by 90%, we assume a value of 0.5×10^{-6} (corresponding to 0.5 predators per 100 m^2). These parameters produce the relationship between predator density (evaluated as number of predators in a 10×10 m^2) and relative survival of aquatic predation illustrated in Figure A.4.

A.2.13 MOVEMENT BARRIERS: REMOVED

The previous version of the trout model (Railsback and Harvey 2001) included simulation of barriers to upstream movement by fish (e.g., waterfalls). Given the absence of such barriers in the Green River below Flaming Gorge, we removed this capability.

A.2.14 SPAWNING DECISION: CHANGE IN FLOW

The trout model assumes that adult trout will not spawn if the change in flow (as a fraction of the current flow) is above the value specified by the parameter *fishSpawnMaxFlowChange*. In previous model versions, this change in flow was the change in daily mean flow. We retain the assumption that trout base spawning decisions on daily flows instead of hourly flows, for two reasons: (1) it seems biologically reasonable, and (2) spawning simulations occur once per day, not every time the flow changes significantly.
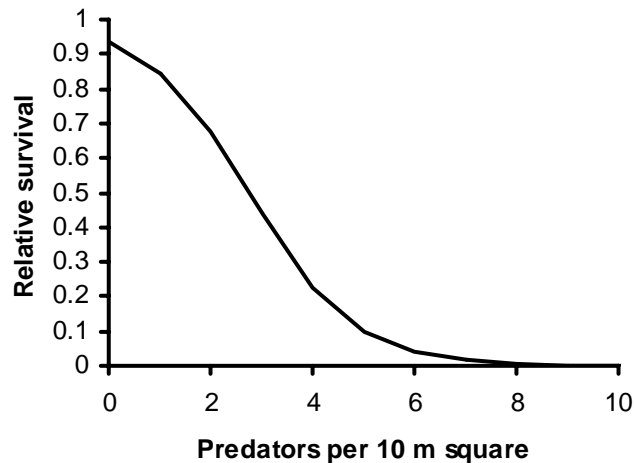
FIGURE A.4 Relationship between Survival and Predator Density

A.2.15 REDD MODEL CHANGES

We make no changes to the trout redd model formulation except for specifying the time step used for input to some of the redd model processes. Redd events are simulated once per day, at the first hour of daytime, and use daily habitat variables. The redd simulations conducted at the start of a new daytime phase represent events occurring over the current full day (from midnight to hour 23).

A.2.15.1 Flow Variable for Scouring Survival

Mortality of redds due to scouring or filling when the river bed moves is a function of peak flow. Therefore, the scouring survival function uses as its input the *maximum* daily flow.

The scouring survival function is executed whenever the flow peaks. In the previous model version that used daily mean flows, a flow peak is identified as occurring if the current day's flow is greater than both the past day's and the next (future) day's flow. In the Green River version, we use the same procedure, except that we used the maximum hourly flow for each day. Scouring survival calculations are triggered if the maximum hourly flow for the current day is greater than the maximum hourly flow of the preceding day and greater than the maximum hourly flow of the next day.

A.2.15.2 Flow for Dewatering Survival

Dewatering mortality occurs when the water surface elevation drops below the bottom elevation of the cell containing a redd, exposing the redd to the air. The degree of mortality depends on the duration of dewatering (eggs gradually die over time when dewatered), so this redd survival function varies with the time scale of the flow. Because we developed this survival function for previous models that used daily mean flows, we continue to use the depth at mean daily flow to determine dewatering survival. Dewatering mortality is a relatively slow process (redds typically retain enough moisture that short dewaterings may have little effect), so use of a daily time step is appropriate.

A.2.15.3 Temperature Variable for Survival Functions

There are separate redd survival functions for extremely low and high temperatures. The mortality of eggs resulting from an extreme temperature is a function of the duration of exposure—short exposures to extreme temperatures may kill few if any eggs, but mortality is expected to increase over time. Because our temperature survival functions were designed for daily time steps, and because mortality occurs relatively slowly at realistic temperatures, we continue to use the daily mean temperature to evaluate redd survival.

A.2.16 INITIAL LOCATIONS EXCLUDING EXTREME VELOCITIES

Previous versions of the model were initialized by creating fish and placing them randomly in cells; only dry cells were excluded as initial locations. This process worked well for small streams, where even small trout can find good habitat before being killed by high-velocity mortality. However, the Green River has extensive areas of high velocity, and small trout initially placed in such habitat often cannot move far enough to escape high-velocity mortality, resulting in a burst of mortality at the start of a simulation.

To avoid this problem, we modified the initialization routine to exclude as an initial location any cell with velocity greater than that posing a 90% daily survival probability (10% mortality risk). This velocity is calculated as the trout parameter *mortFishVelocityV9* times the new trout's maximum swim speed.

A.2.17 MINOR CHANGES TO IMPROVE EXECUTION SPEED

Because the Green River model simulates thousands of fish examining hundreds of habitat cells, the execution time of the model's software is a significant concern. We made several minor changes to the formulation that speed up execution; these should have a negligible effect on simulation results.

Unlike previous model versions, we hardwired into the software the assumption that temperature is constant among habitat cells. (This assumption was already made by the model formulation.) This allowed us to significantly reduce the number of computations calculating a trout's maximum food intake rate (C_{max}) and standard respiration.

The logistic functions used to simulate survival probabilities produce values asymptotically approaching zero or one for many input values. We assumed that function input producing values less than 0.000000002 are equal to 0.0, and that input producing values greater than 0.999999998 are equal to 1.0. This assumption reduces computations and avoids floating point over- and underflow errors.

The trout movement method was altered to reduce the number of habitat cells that trout evaluate as potential movement destinations. After identifying all of the cells that are potential destinations (because they are within the radius that defines potential destinations), a trout sequentially calculates its fitness measure (Section A.2.5) for each cell. This evaluation uses up the most computer time, so execution speed can be increased by eliminating obviously bad cells with as little evaluation as possible. However, we must be careful not to eliminate cells that may be bad but still the best available cells during adverse conditions. One category of cells that is very unlikely to include the best cells is that corresponding to very high velocities, because extreme velocities result in highly negative growth and high risk of high-velocity mortality. Keeping in mind that a fish's swimming speed is reduced if it uses velocity shelters for feeding, model trout eliminate as destination cells any that meet the inequality:

$$\frac{cellVelocity \times fishShelterSpeedFrac}{maxSwimSpeed} > mortFishVelocityV9$$

where *fishShelterSpeedFrac* is the trout parameter for the fraction by which swimming speed is reduced if the fish is using a velocity shelter (0.5 in the Green River model), *maxSwimSpeed* is the trout's maximum sustainable swimming speed, and *mortFishVelocityV9* is the trout parameter defining the ratio of swimming speed to *maxSwimSpeed* at which daily survival of high-velocity mortality is 0.9. Cells meeting this inequality are put on a temporary list of bad destination cells.

To ensure that the trout has found a destination cell better than any on the list of bad destinations, a check is made. If the fitness measure (Section A.2.5) for the best cell is lower than the highest possible fitness measure for any of the bad destination cells, then all cells on the bad destination list are also evaluated fully. This highest fitness measure for bad destination cells is:

$$[0.9 + (0.1 \times mortFishVelocityCoverFactor)]^{timeHorizon}$$

which assumes the trout is using hiding cover in a cell with velocity that makes its (non-hiding) risk of high-velocity mortality equal to 0.9.

A.3 MODEL INPUT FOR THE GREEN RIVER

This section describes the trout model input used at the Green River study sites. There are five general kinds of input to the model.

- Trout parameters: coefficients for the equations used to model trout. Parameter values may vary among trout species, and a few parameters (especially those defining mortality risks) may vary among sites.

- Habitat parameters: coefficients for the equations used to model habitat. Values for many of these parameters vary among sites.

- Habitat data: site-specific data describing the characteristics of each habitat cell.

- Fish data: characteristics of the trout populations at each site, used to initialize, calibrate, and test the model.

- Driving variables: the time series of flow, temperature, and turbidity used by the model.

Guidance on input formats, etc., is provided in the trout model's user guide, a separate (unpublished) document. This section provides a complete list of input requirements and documents the input values currently being used for the Green River study sites.

A.3.1 TROUT PARAMETERS

Table A.4 provides a summary of all trout parameters in the model. For most parameters, the same value is used for all trout species, and the basis of the value is provided by Railsback and Harvey (2001). Other parameters (with their names underlined) must have their values determined for the Green River model because they are new in Version 3 of *inSTREAM*, differ among species, or are site-specific. Values for new parameters were explained in Section A.2. The values for species- or site-specific parameters are explained in the table.

In determining whether parameter values differ among the trout species in the model, our approach was to assume no differences unless we were aware of literature showing that differences among species are significant in comparison to the uncertainty in the parameter value.

The simulation experiments used to evaluate fluctuating flow effects were simplified by assuming all trout belonged to the same species (which used the rainbow trout parameter values) and by neglecting spawning and angler harvest. Hence, parameters in Table A.4 or cutthroat and brown trout, and for spawning, redds, and angler harvest, were not used in the experiments.

TABLE A.4 Definition, Value, and Basis for Trout Parameters

Parameter	Definition	Units	Value and Basis
fishCmaxParamA	Allometric constant in maximum intake equation.	d^{-1}	0.628
fishCmaxParamB	Allometric exponent in maximum intake equation.	None	−0.3
fishCmaxTempF1	Function value for point 1 in the C_{max} temperature function.	None	0.05
fishCmaxTempF2	Function value for point 2 in the C_{max} temperature function.	None	0.05
fishCmaxTempF3	Function value for point 3 in the C_{max} temperature function.	None	0.5
fishCmaxTempF4	Function value for point 4 in the C_{max} temperature function.	None	1.0
fishCmaxTempF5	Function value for point 5 in the C_{max} temperature function.	None	0.8
fishCmaxTempF6	Function value for point 6 in the C_{max} temperature function.	None	0.0
fishCmaxTempF7	Function value for point 7 in the C_{max} temperature function.	None	0.0
fishCmaxTempT1	Temperature for point 1 in the C_{max} temperature function.	°C	0.0
fishCmaxTempT2	Temperature for point 2 in the C_{max} temperature function.	°C	2.0
fishCmaxTempT3	Temperature for point 3 in the C_{max} temperature function.	°C	10
fishCmaxTempT4	Temperature for point 4 in the C_{max} temperature function.	°C	22
fishCmaxTempT5	Temperature for point 5 in the C_{max} temperature function.	°C	23
fishCmaxTempT6	Temperature for point 6 in the C_{max} temperature function.	°C	25
fishCmaxTempT7	Temperature for point 7 in the C_{max} temperature function.	°C	100
fishEnergyDensity	Factor to convert net energy intake to growth.	j/g	5,900
fishFecundParamA	Fecundity multiplier.	eggs/redd	0.109
fishFecundParamB	Fecundity exponent.	None	2.54
fishFitnessHorizon	Time horizon for Expected Reproductive Maturity fitness measure.	d	90

TABLE A.5 (Cont.)

Parameter	Definition	Units	Value and Basis
fishMoveDistParamA	Multiplier for maximum movement distance.	None	200 for all species Basis: distance reduced from previous versions due to shorter time step and wider river (which makes more stream area available within a certain radius). A 5-cm trout can move 10 m; a 50-cm trout can move 100 m.
fishMoveDistParamB	Exponent for maximum movement distance.	None	1.0
fishMovePenaltyTime	Time for which feeding does not occur after a fish moves.	h	0.25
fishPiscivoryLength	The length at which trout become piscivorous.	cm	Rainbow and cutthroat: 40 Brown: 25 Basis: see Section A.2.1.2.
fishReactDistNightFactor	Multiplier applied to reactive distance at night.	None	0.5 for all species Basis: see Section A.2.2.1.
fishReactParamA	Constant in reactive distance equation.	None	–5.91
fishReactParamB	Velocity parameter for reactive distance.	None	0.847
fishReactParamC	Temperature parameter for reactive distance.	1/°C	–0.0473
fishReactParamD	Fish length parameter for reactive distance.	None	1.74
fishRespParamA	Allometric constant in standard respiration equation.	$j/d \times g^{-0.78}$	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
fishSearchArea	Area that a fish searches for stationary food.	cm^2	20,000
fishSearchNightFactor	Fraction (0–1) by which search feeding intake is reduced at night.	None	0.5 for all species Basis: see Section A.2.2.2.

TABLE A.5 (Cont.)

Parameter	Definition	Units	Value and Basis
fishShelterSpeedFrac	Swim speed multiplier for fish using velocity shelter.	None	0.5
			Field observations show substrates at study sites are embedded and provide incomplete velocity shelter.
fishSpawnDSuitD1	Depth for point 1 on depth function for spawning habitat suitability.	cm	0.0
fishSpawnDSuitD2	Depth for point 2 on depth function for spawning habitat suitability.	cm	5.0
fishSpawnDSuitD3	Depth for point 3 on depth function for spawning habitat suitability.	cm	50.0
fishSpawnDSuitD4	Depth for point 4 on depth function for spawning habitat suitability.	cm	100.0
fishSpawnDSuitD5	Depth for point 5 on depth function for spawning habitat suitability.	cm	1,000.0
fishSpawnDSuitS1	Function value for point 1 on depth function for spawning habitat.	None	0.0
fishSpawnDSuitS2	Function value for point 2 on depth function for spawning habitat.	None	0.0
fishSpawnDSuitS3	Function value for point 3 on depth function for spawning habitat.	None	1.0
fishSpawnDSuitS4	Function value for point 4 on depth function for spawning habitat.	None	1.0
fishSpawnDSuitS5	Function value for point 5 on depth function for spawning habitat.	None	0.0
fishSpawnEndDate	Date on which spawning ends.	day	Rainbow and cutthroat trout: May 31 Brown trout: December 1 Basis: literature estimates.
fishSpawnMaxFlow	The maximum flow at which trout will spawn.	m^3/s	All species and sites: 100 Basis: estimate.
fishSpawnMaxFlowChange	Maximum change in daily flow for spawning.	None	0.2
fishSpawnMaxTemp	Maximum temperature for spawning.	°C	Rainbow and cutthroat: 13 Brown: 10 Basis: estimated by Van Winkle et al. (1996) from literature for rainbow and brown trout.
fishSpawnMinAge	Minimum age for spawning.	years	1

TABLE A.5 (Cont.)

Parameter	Definition	Units	Value and Basis
fishSpawnMinCond	Minimum condition factor for spawning females.	None	0.95
fishSpawnMinLength	Minimum length for spawning.	cm	25 for all species Estimate based on size of age 1 trout.
fishSpawnMinTemp	Minimum temperature for spawning.	°C	Rainbow and cutthroat: 8 Brown: 4 Basis: values estimated by Van Winkle et al. (1996) from literature for rainbow and brown trout.
fishSpawnProb	Probability of spawning on days when all spawning criteria are met.	None	0.011
fishSpawnStartDate	Date on which spawning starts.	day	Rainbow and cutthroat: April 1 Brown: October 1 Basis: literature estimates.
fishSpawnVSuitS1	Suitability for point 1 on velocity function for spawning habitat suitability.	None	0.0
fishSpawnVSuitS2	Suitability for point 2 on velocity function for spawning habitat suitability.	None	0.0
fishSpawnVSuitS3	Suitability for point 3 on velocity function for spawning habitat suitability.	None	1.0
fishSpawnVSuitS4	Suitability for point 4 on velocity function for spawning habitat suitability.	None	1.0
fishSpawnVSuitS5	Suitability for point 5 on velocity function for spawning habitat suitability.	None	0.0
fishSpawnVSuitS6	Suitability for point 6 on velocity function for spawning habitat suitability.	None	0.0
fishSpawnVSuitV1	Velocity for point 1 on velocity function for spawning suitability.	cm/s	0.0
fishSpawnVSuitV2	Velocity for point 2 on velocity function for spawning suitability.	cm/s	10.0
fishSpawnVSuitV3	Velocity for point 3 on velocity function for spawning suitability.	cm/s	20.0

TABLE A.5 (Cont.)

Parameter	Definition	Units	Value and Basis
fishSpawnVSuitV4	Velocity for point 4 on velocity function for spawning suitability.	cm/s	75.0
fishSpawnVSuitV5	Velocity for point 5 on velocity function for spawning suitability.	cm/s	100.0
fishSpawnVSuitV6	Velocity for point 6 on velocity function for spawning suitability.	cm/s	1,000.0
fishSppDomFactor	Multiplier representing effect of species on length-dependent dominance.	None	1.0
fishSwimParamA	Length coefficient for maximum sustainable swim speed.	1/s	1.83
fishSwimParamB	Constant in equation for maximum swim speed.	cm/s	33.0
fishTurbidMin	Turbidity below which reactive distance is unaffected.	Nephelometric Turbidity Unit [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
fishWeightParamA.	Multiplier in length-weight relationship.		Rainbow: 0.0185 Brown: 0.0157 Cutthroat: 0.0089 Basis: see Section A.3.1.1.
fishWeightParamB	Exponent in length-weight relationship.	None	Rainbow: 2.90 Brown: 2.91 Cutthroat: 3.09 Basis: see Section A.3.1.1.
mortFishAngleFracKeptIllegal	The fraction of hooked fish not of legal length that are kept by anglers.	None	0.05 for all species Basis: see Section A.2.11.
mortFishAngleFracKeptLegal	The fraction of hooked fish of legal length that are kept by anglers.	None	0.2 for all species Basis: see Section A.2.11.
mortFishAngleHookSurvRate	Fraction of released trout that survive.	None	0.8 for all species Basis: see Section A.2.11.
mortFishAngleL1	Fish length at which relative risk of being hooked is 10% of maximum.	cm	10 for all species Basis: see Section A.2.11.
mortFishAngleL9	Length at which hooking risk is 90% of maximum.	cm	20 for all species Basis: see Section A.2.11.
mortFishAngleSlotLower	Length defining the lower end of the range in which fish are illegal to keep.	cm	33 for all species Basis: Utah fishing regulations.

TABLE A.5 (Cont.)

Parameter	Definition	Units	Value and Basis
mortFishAngleSlotUpper	Length defining the upper end of the range in which fish are illegal to keep.	cm	51 for all species Basis: Utah fishing regulations.
mortFishAngleSuccess	Multiplier to determine capture probability from fishing pressure.	(angler-h)$^{-1}$	0.01 for all species Basis: see Section A.2.11.
mortFishAqPredA1	Density of active piscivores at which aquatic predation survival is increased only 10% above the minimum.	piscivorous fish per cm^2	5×10^{-6} for all species Basis: see Section A.2.12.
mortFishAqPredA9	Density of active piscivores at which aquatic predation survival is increased 90% above the minimum.	piscivorous fish per cm^2	0.5×10^{-6} for all species Basis: see Section A.2.12.
mortFishAqPredCoverFactor	Aquatic predation survival increase factor for fish using hiding cover.	None	0.95 for all species Basis: see Section A.2.4.2.
mortFishAqPredD1	Depth at which depth survival increase function for aquatic predation is 10% of maximum.	cm	25.0
mortFishAqPredD9	Depth at which depth survival increase function for aquatic predation is 90% of maximum.	cm	10.0
mortFishAqPredDayMin	Minimum aquatic predation survival probability for fish in daytime.	None	0.997 for all species Basis: see Section A.2.3.2.
mortFishAqPredL1	Length at which fish length survival increase function for aquatic predation is 10% of maximum.	cm	4.0
mortFishAqPredL9	Length at which fish length survival increase function for aquatic predation is 90% of maximum.	cm	8.0
mortFishAqPredNightMin	Minimum aquatic predation survival probability for fish at night.	None	0.996 for all species Basis: see Section A.2.3.2.
mortFishAqPredT1	Temperature at which aquatic predation survival is increased only 10%.	°C	6.0
mortFishAqPredT9	Temperature at which aquatic predation survival is increased 90%.	°C	2.0
mortFishAqPredU1	Turbidity at which aquatic predation survival is increased only 10%.	NTU	5.0
mortFishAqPredU9	Turbidity at which aquatic predation survival is increased 90%.	NTU	80.0
mortFishConditionK1	Condition factor at which daily survival probability is 0.1.	None	0.2 Basis: calibration: Section A.4.3.

TABLE A.5 (Cont.)

Parameter	Definition	Units	Value and Basis
mortFishConditionK9	Condition factor at which daily survival probability is 0.9.	None	0.5 Basis: calibration: Section A.4.3.
mortFishVelocityHideFactor	Survival increase factor for fish using hiding cover, for high velocity mortality.	None	0.75
mortFishSpawn	The probability of surviving spawning mortality.	None	0.9
mortFishStrandD1	The ratio of depth to fish length at which survival of stranding is 10%.	None	–0.3[a]
mortFishStrandD9	The ratio of depth to fish length at which survival of stranding is 90%.	None	0.3
mortFishTerrPredCoverFactor	Terrestrial predation survival increase factor for fish using hiding cover.	None	0.99 Basis: calibration: Section A.4.3.
mortFishTerrPredD1	Depth at which terrestrial predation survival is increased only 10%.	cm	50 Diving predators (mergansers, otters) are common, so depth offers less refuge.
mortFishTerrPredD9	Depth at which terrestrial predation survival is increased 90%.	cm	1,000 Basis: depth offers less refuge from predators like otters. (Section A.4.3)
mortFishTerrPredDayMin	The minimum daily survival probability for terrestrial predation during day.	None	Value for all species: 0.99 Basis: see Section A.2.3.1; calibration in Section A.4.3.
mortFishTerrPredH1	Distance to hiding cover at which terrestrial predation survival is increased only 10%.	cm	500
mortFishTerrPredH9	Distance to hiding cover at which terrestrial predation survival is increased 90%.	cm	–100[b]
mortFishTerrPredL1	Fish length at which terrestrial predation survival is increased 10%.	cm	6.0
mortFishTerrPredL9	Fish length at which terrestrial predation survival is increased 90%.	cm	3.0
mortFishTerrPredNightMin	The minimum daily survival probability for terrestrial predation at night.	None	Preliminary value for all species: 0.997 Basis: see Section A.2.3.1; calibration: Section A.4.3.
mortFishTerrPredT1	Turbidity at which terrestrial predation survival is increased 10%.	NTU	10.0

TABLE A.5 (Cont.)

Parameter	Definition	Units	Value and Basis
mortFishTerrPredT9	Turbidity at which aquatic predation survival is increased 90%.	NTU	50.0
mortFishTerrPredV1	Velocity at which terrestrial predation survival is increased 10%.	cm/s	20.0
mortFishTerrPredV9	Velocity at which terrestrial predation survival is increased 10%.	cm/s	300 Basis: in large river, velocity offers less protection from predators like otters (see Section A.4.3).
mortFishVelocityV1	Ratio of cell velocity to fish's maximum sustainable swim speed, at which high velocity survival is 10%.	None	1.8
mortFishVelocityV9	Ratio of cell velocity to fish's maximum sustainable swim speed, at which high velocity survival is 90%.	None	1.4
mortFishVelocityCoverFactor	Fraction by which survival of high velocity survival is increased if fish is using hiding cover.	None	0.75 Basis: see Section A.2.4.2.
mortReddDewaterSurv	Daily fraction of eggs that survive dewatering.	None	0.9
mortReddHiTT1	Temperature at which high temperature survival of eggs is 10%.	°C	Rainbow and cutthroat: 30 Brown: 25 Basis: Railsback et al. 1999.
mortReddHiTT9	Temperature at which high temperature survival of eggs is 90%.	°C	Rainbow and cutthroat: 21 Brown: 16 Basis: Railsback et al. 1999.
mortReddLoTT1	Temperature at which low temperature survival of eggs is 10%.	°C	Rainbow and cutthroat: –3 Brown: –0.8 Basis: Railsback et al. 1999.
mortReddLoTT9	Temperature at which low temperature survival of eggs is 10%.	°C	All species: 0 Basis: Railsback et al. 1999.
mortReddScourDepth	Depth of scour or fill that destroys a redd.	cm	10.0
mortReddShearParamA	Multiplier for the relationship between flow and shear stress.	s/m^3	0 Eliminates scouring redd mortality; considered unimportant for Green River.
mortReddShearParamB	Exponent for the relationship between flow and shear stress.	None	0.11

TABLE A.5 (Cont.)

Parameter	Definition	Units	Value and Basis
reddDevelParamA	Constant in daily redd development equation.	None	Rainbow and cutthroat: –0.000253 Brown: 0.00313 Basis: Van Winkle et al. 1996.
reddDevelParamB	Temperature coefficient in daily redd development equation.	$°C^{-1}$	Rainbow and cutthroat: 0.00134 Brown: 3.07×10^{-5} Basis: Van Winkle et al. 1996.
reddDevelParamC	Temperature squared coefficient in daily redd development equation.	$°C^{-2}$	Rainbow and cutthroat: 3.21×10^{-5} Brown: 9.34×10^{-5} Basis: Van Winkle et al. 1996.
reddNewLengthMean	Mean length of new fish upon emergence.	cm	2.8
reddNewLengthStdDev	Standard deviation in length of new fish.	cm	0.2
reddSize	Mean area of a redd.	cm^2	700

[a]   This value is based on the mathematical function used to describe the relationship between depth and survival. Although a ratio less than 0 is not theoretically possible, –0.3 is the value that would produce a 10% survival rate.

[b]   This value is based on the mathematical function used to describe the relationship between distance to hiding cover and survival. Although a distance less than 0 is not theoretically possible, –100 is the value that would produce a 90% increase in survival.

A.3.1.1 Length-Weight Parameters

Two parameters (*fishWeightParamA*, *fishWeightParamB*) define a power curve of "healthy" weight as a function of length. These parameters were developed from electrofishing data collected by Utah Department of Wildlife Resources (UDWR) in 1997–2000. Lengths and weights of individual fish were provided to us by UDWR, for spring and fall samples at the Tailwater and Little Hole sites. From these data, we estimated parameters for each species (but not separate values for each site) using the following steps:

- Data for each species were analyzed separately, but data for all ages, sites, and dates were analyzed together.

- The measured total trout length was converted to an estimated fork length using these multipliers from Carlander (1969): rainbow trout: 0.96; brown trout: 0.98; cutthroat trout: 0.95.

- The standard condition factor ($100,000 \times$ weight/length^3) was calculated for each fish by UDWR (using total length). The mean and median condition factors were calculated, leaving out extreme or erroneous values (condition factor >3 or <0.1). For rainbow trout, both mean and median condition factors were 1.04. For brown trout, the mean and median were both 0.98. For cutthroat, the mean was 0.97 and the median was 0.95.

- Fish with normal to relatively high condition factors were selected for regression analysis. Estimated fork lengths were converted from mm to cm. Regression of weight vs. length produced the length-weight parameter values in Table A.4. For rainbow trout, fish with condition factors between 1.04 and 2.0 were used (n = 2,452 fish). For brown trout, fish with condition factors between 0.98 and 2.0 were used (n = 2,674 fish). Cutthroat with condition factors between 0.97 and 2.0 were used (n = 108 fish).

A.3.2 HABITAT PARAMETERS

The trout model uses the parameters in Table A.5 to represent habitat. Habitat parameters are generally specific to the site being modeled, and the food production parameters are typically evaluated by using them to calibrate trout growth and production. Because angler mortality was neglected in the flow fluctuation experiments, angling parameters are currently only initial estimates.

A.3.3 HABITAT DATA

Habitat data were developed for four study sites: Indian Crossing, Little Hole, Pipe Creek, and Tailrace. These inputs were developed from PHABSIM instream flow studies conducted in about 1988 by the U.S. Fish and Wildlife Service and the Utah Division of Wildlife Resources (Hann et al. 1991).

A.3.3.1 Cell Characteristics

Each habitat cell has values for the following variables that are constant over time:

- Coordinates defining the cell's location and size.

- Fraction of cell area providing velocity shelters for drift feeding.

- Mean distance to hiding cover.

TABLE A.5 Definition, Value, and Basis for Habitat Parameters

Parameter	Definition	Units	Value and Basis
habAnglePressJan	Angling pressure in January.	angler-h/d/km	2.0
habAnglePressFeb	Angling pressure in February.	angler-h/d/km	2.0
habAnglePressMar	Angling pressure in March.	angler-h/d/km	5.0
habAnglePressApr	Angling pressure in April.	angler-h/d/km	10.0
habAnglePressMay	Angling pressure in May.	angler-h/d/km	25.0
habAnglePressJun	Angling pressure in June.	angler-h/d/km	75.0
habAnglePressJul	Angling pressure in July.	angler-h/d/km	100.0
habAnglePressAug	Angling pressure in August.	angler-h/d/km	100.0
habAnglePressSep	Angling pressure in September.	angler-h/d/km	75.0
habAnglePressOct	Angling pressure in October.	angler-h/d/km	50.0
habAnglePressNov	Angling pressure in November.	angler-h/d/km	10.0
habAnglePressDec	Angling pressure in December.	angler-h/d/km	5.0
habAnglePressNightFactor	Night fishing pressure as a fraction of daytime pressure.	None	0.0 except for 0.05 at Little Hole site Basis: see Section A.2.11.
habDriftConc	Concentration of drifting food items.	g/cm^3	1.5×10^{-10} Basis: see Section A.4.1.1. (Preliminary calibration produced no change: Section A.4.3.)
habDriftRegenDist	Distance over which drift food is replenished.	cm	250 Basis: see Section A.4.1.1.
habFracFlowChangeForMovement	The fractional change in river flow that triggers trout movement simulations.	None	0.1 Basis: see Section A.2.1.2.
habLatitude	Latitude of the study site.	degrees	41
habPreyEnergyDensity	Energy density of food items.	j/g	4,000 Basis: see Section A.4.1.1.
habSearchProd	Areal production rate for stationary food items.	g/cm^2/h	1.0×10^{-6} Basis: see Section A.4.1.1.
habTwilightLength	Amount of time before sunrise and after sunset that is best represented as daytime.	h	0.5 Basis: estimate

- Fraction of cell providing hiding cover for adult trout.

- Fraction of cell area having substrate suitable for spawning.

Cell coordinates were developed from the "IFG4" hydraulic model input files from the PHABSIM study. Each study site included several hundred meters of river length, represented by a small number of transects (Table A.6). One very important limitation of using the PHABSIM data for the trout model's habitat input is that the number of transects is too small to represent the site's habitat diversity, which is a problem typical of PHABSIM studies. The only way to overcome this limitation is by collecting new habitat data at the study sites, which this project was not able to do.

A second concern with using PHABSIM data for habitat input is the spatial resolution of the cells. Analysis of spatial scales used by trout indicates that cells should have the length and width of one to several meters (Railsback and Harvey 2001). The Green River PHABSIM data used cells typically 3 m in width, which is reasonable for the trout model. However, the small number of transects that each represent many meters of habitat produced PHABSIM cells many tens of meters in length, which is much longer than desirable. (Of particular concern is the model's assumption of hierarchical competition for food within each cell; larger cells tend to allocate more food to large trout and less to small trout, compared to the same area divided into smaller cells.) To reduce scaling errors that result from the large cell lengths, transects were divided to produce cell lengths of 10–20 m (Table A.6).

Observations of cell habitat variables (fraction of cell with velocity shelters, hiding cover, and spawning gravel; distance to hiding cover) were made by G. Burton, J. Hayse, K. LaGory, and S. Railsback on October 1 to 3, 2001. These observations were made by approximately locating the original PHABSIM transects, then estimating values at a number of points throughout the PHABSIM reach. Measurement locations were recorded as GPS coordinates and were marked on aerial photographs of the reach. Values were estimated visually from a raft, from shore, and while wading. These observations used the ordinary high water mark as a shoreline reference; the locations of high water shorelines in the habitat model were determined by simulating the ordinary high flow of 130 m^3/s.

TABLE A.6 Study Site Length and Number of Transects

Site	Site Length (m)*	Number of Transects in PHABSIM Model (average cell length, m)	Number of Transects in Individual-based Trout Model (average cell length, m)
Indian Crossing	494	6 (82)	19 (20)
Little Hole	404	6 (67)	21 (19)
Pipe Creek	482	10 (48)	26 (19)
Tailrace	204	6 (34)	21 (10)

* The length reported here is greater than the site lengths reported by Hann et al. (1991) because we assumed the first transect also represented some distance downstream of itself, and the last transect represented some distance upstream.

The values of hiding cover variables determined from the October 2001 field observations include the cover provided by algae and macrophytes. Aquatic vegetation was common and sometimes dense at many locations, providing extensive and abundant hiding cover. Especially because there is little other hiding cover in much of the Green River trout reach, the vegetation cover is too important to neglect. However, vegetation cover undoubtedly changes with season and could be considerably reduced in winter. Considering the complexity of modeling vegetation dynamics and the other limitations of our habitat input, we currently assume that cover variables observed in October 2001 are constant even though much of the cover was provided by vegetation.

A.3.3.2 Cell Hydraulics

Input for simulating hydraulics (how depth and velocity in each cell varies with river flow) is provided to *inSTREAM-SD* as a lookup table generated by an external PHABSIM hydraulic model. For the four Green River study sites, we used the MANSQ hydraulic simulation approach as implemented in the RHABSIM 2.0 version of PHABSIM produced by Thomas R. Payne Assoc. The hydraulic simulation approach we used is designed to circumvent some of the limitations of other PHABSIM approaches (EPRI 2000). The following steps were taken in producing the cell hydraulic input to the trout model from the IFG4 input files used in the 1988 PHABSIM study:

- The calibration velocities were edited to convert negative velocities to positive ones, because the trout model uses absolute velocities; the direction of flow does not matter. Using our hydraulic calibration methods, changing negative velocities to positive has little, if any, effect on simulation accuracy.

- The IFG4 files for each site were imported into RHABSIM and conversion was made from English to metric units.

- For the Tailrace and Little Hole sites, we determined that left and right banks in the IFG4 files needed to be reversed to provide an accurate map of the habitat. This was accomplished by exporting the files from RHABSIM in RHABSIM's text file format, editing the text file in a spreadsheet to reverse the order of the cell data, and importing the file back into RHABSIM. (The cell data file that defines cell boundaries and habitat variables was likewise reversed.)

- The regression method was chosen to predict water surface elevation (WSE) from flow. With one exception among all transects of all three sites, WSE was predicted well as a log-linear function of flow.

- Calibration velocities in each cell were provided for three flows. Each of the three calibration sets was used to simulate cell velocities over a range of flows around the calibration value (Table A.7). The MANSQ approach uses the

TABLE A.7 Hydraulic Calibration Flows and Ranges

IFG4 Calibration Velocity Set	Calibration Flow, m^3/s	Range of Flows Simulated Using the Calibration Set, m^3/s
Indian Crossing 3	25	10–30
Indian Crossing 2	71	35–80
Indian Crossing 1	113	85–300
Little Hole 1	23	10–30
Little Hole 2	68	35–80
Little Hole 3	105	85–300
Pipe Creek 1	25	10–30
Pipe Creek 2	66	35–80
Pipe Creek 3	106	85–300
Tailrace 1	23	10–30
Tailrace 2	71	35–80
Tailrace 3	115	85–300

calibration velocity to fit a calibration parameter ("n") for each cell; "n" is then used to calculate velocities at other flows. Velocities were not adjusted to force the total simulated flow (the sum over all cells on a transect of velocity times depth times cell width) to equal the known flow.

- Simulated velocities over the range of flows were reviewed. In only three cases, the "n" value for a cell was altered to eliminate unrealistic results.

- The simulated velocities were exported from RHABSIM in a format read by the trout model.

A.3.4 INITIAL TROUT POPULATION DATA

Input defining the number and size of trout in each species and age is used to initialize the model. Ideally this input would be derived from field observations made at a site and date close to those being simulated. Data on the Flaming Gorge trout population are available from UDWR; these data were useful for establishing age and size distributions, but not for estimating abundance.

UDWR conducts spring and fall censuses near the Tailrace and Little Hole sites, using night electrofishing in shallow habitat and along shorelines, but not in the deeper water of the main channel. Abundance is estimated using a mathematical transformation of the electrofishing catch per effort data; however, this transformation is believed by UDWR staff to severely overestimate trout density. (The UDWR density estimates range 1–2 trout/m^2 at Little Hole and 2–3 trout/m^2 at Tailrace; these values seem unreasonable and produced rapid starvation when tested in the trout model.) Therefore, initial population data were developed by using the age and size distributions from the UDWR data and abundances reported (but not well documented) by Filbert and Hawkins (1995).

TABLE A.8 Relative Abundance of Rainbow and Brown Trout by Age, from UDWR Electrofishing Data

Age	Relative Abundance, Spring		Relative Abundance, Fall	
	Rainbow	Brown	Rainbow	Brown
0	0.0	0.0	2.0	0.0
1	0.5	0.7	16.0	3.0
2	20.0	3.0	19.0	34.0
3	15.0	26.0	18.0	24.0
4	22.0	34.0	19.0	23.0
5	26.0	29.0	20.0	14.0
6	15.0	7.0	7.0	2.0
7	2.0	0.4	0.6	0.3
8	0.2	0.0	0.0	0.0
9	0.1	0.0	0.1	0.0
10	0.1	0.0	0.0	0.0

Age and length of individual trout were estimated by UDWR in their data from 1997 through 1999. The age data (Table A.8) show that older fish dominate the population, e.g., with age 5 trout being far more abundant than age 1 trout. Long-distance movement is the most feasible explanation for this unusual distribution; trout may be able to compete for the high-quality habitat at these sites only after growing to substantial size further downstream. The length data (Table A.9) show that rainbow and brown trout lengths are similar, and unusually large.

Filbert and Hawkins (1995) reported biomass densities of 840 kg/ha at Tailrace and 500 kg/ha at Little Hole. We used these two values to estimate initial populations at Tailrace and Little Hole, and assumed that the biomass density at Pipe Creek was intermediate (670 kg/ha) and was half the Tailrace value (420 kg/ha) at Indian Crossing. These biomass values were allocated among ages using the relative abundance (Table A.8) and length data (Table A.9) (along with the trout length-weight relationship and the area of each study site), to produce the initial fish population characteristics (Table A.10). These are the values used in the flow fluctuation simulation experiments, which treat all trout as one species.

TABLE A.9 Length (cm) of Rainbow and Brown Trout by Age, from UDWR Electrofishing Data

	Mean (S.D.) Length, Spring		Mean (S.D.) Length, Fall	
Age	Rainbow	Brown	Rainbow	Brown
0			24.3 (2)	
1	25.5 (5)	14.0 (3)	27.3 (4)	25.2 (3)
2	29.0 (3)	26.7 (8)	27.5 (5)	41.1 (3)
3	35.5 (3)	40.3 (4)	35.1 (5)	42.4 (7)
4	38.0 (3)	42.7 (4)	39.3 (3)	45.4 (4)
5	40.1 (3)	44.9 (4)	41.0 (4)	44.0 (4)
6	43.0 (3)	59.7 (2)	40.8 (4)	47.1 (3)
7	43.0 (6)		41.7 (8)	47.9 (*)
8	43.7 (4)			
9	63.0 (*)		46.6 (*)	
10	37.0 (*)			

*   Only one individual in this category was observed.

TABLE A.10 Initial Population Input

Age	Mean Length (cm)	Length Standard Deviation (cm)	Number of Initial Trout			
			Indian Crossing	Little Hole	Pipe Creek	Tailrace
0	12	1	18	33	48	18
1	26	4	137	260	377	137
2	28	4	226	430	624	226
3	35	4	200	380	551	200
4	39	3	207	393	570	207
5	41	3	200	380	551	200
6	42	4	65	123	179	65
Total			1,050	2,000	2,900	1,050

A.4 CALIBRATION AND VALIDATION

This section describes how the trout model was calibrated for the Green River sites and then tested with respect to its key behaviors. Because of the model's complexity, it is impossible to calibrate more than a very small number of parameters using the full IBM. Instead, we use an incremental approach, starting by calibrating separate submodels (especially feeding and growth), then making sure that the full model produces results that are reasonable in several very basic ways, and finally testing whether the IBM can reproduce observed patterns of diel habitat and behavior selection.

A.4.1 CALIBRATION OF FOOD AND FEEDING

The first calibration step is finding reasonable values for habitat and fish parameters related to food availability and feeding. The two main issues are (a) how much food production is reasonable for the Green River sites, and (b) what are reasonable values for the fish parameters that determine how feeding is reduced at night.

A.4.1.1 Food Parameters

For its application to Little Jones Creek (Railsback and Harvey 2001), Version 2 of *inSTREAM* used calibrated food parameter values of:

- *habSearchProd* (production rate of search food, g/cm^2/hr): 7.0×10^{-7};

- *habDriftConc* (food concentration in the drift, g/cm^3): 1.50×10^{-10}; and

- *habDriftRegenDist* (distance over which drift is regenerated, cm): 500.

In addition, the Little Jones version used a value of 2,500 j/g for *habPreyEnergyDensity*, the energy content of prey.

Little Jones Creek is an unusually infertile stream, whereas the Green River sites are unusually productive. Filbert and Hawkins (1995) measured drift concentrations in riffles near the Tailrace and Little Hole sites during the day and night and over all four seasons. Year-round average concentrations were roughly 3 mL/100 m^3 at Tailrace and 8 mL/100 m^3 at Little Hole. These values correspond (assuming a density of 1 g per mL for drift invertebrates) to 3.0×10^{-8} g/cm^3 and 8.0×10^{-8} g/cm^3, respectively. However, drift concentration is a poor indicator of food production because drift concentrations are greatly reduced by consumption by fish. The parameter *habDriftRegenDist* better represents production of drift food; smaller values of this parameter indicate that food eaten by trout is replenished more quickly. In addition, the calibrated value of drift concentration also reflects uncertainty in the whole food and feeding formulation.

Considering this information, especially the high productivity of the Green River sites, we selected the following food parameter values to represent an approximate doubling of food production compared to Little Jones Creek:

- *habSearchProd* (production rate of search food, g/cm^2/hr): 1.0×10^{-6};

- *habDriftConc* (food concentration in the drift, g/cm^3): 1.50×10^{-10}; and

- *habDriftRegenDist* (distance over which drift is regenerated, cm): 250.

We also increased the value of *habPreyEnergyDensity*. The value of 2,500 j/g was taken from Van Winkle et al. (1996) and approximates an average value for insect larvae (Hanson et al. 1997). However, trout below Flaming Gorge were found by Filbert (1991) to feed largely on high-energy prey such as amphipods and ephemeroptera. For *habPreyEnergyDensity*, we therefore use a value of 4,000 j/g that is more characteristic of these invertebrates (Hanson et al. 1997).

A.4.1.2 Night Feeding Parameters

The parameters that reduce feeding at night, *fishReactDistNightFactor* and *fishSearchNightFactor*, are new to this version of the trout IBM. From the (meager) literature, we selected values of 0.5 for both of these parameters (Section A.2.2). To test these parameter values, we implemented the feeding and growth formulation in a spreadsheet and calculated the growth (hourly relative growth, grams of growth per hour per gram of body weight) for night conditions, as a function of water velocity and fish length. These calculations were repeated for drift and search feeding at a typical summer temperature of 12ºC.

Our primary criterion for this calibration step was that even at summer temperatures growth at night should be positive for all fish for at least a few velocities. This criterion is based on observations by Green River fisheries managers that night-time feeding is relatively common.

Figure A.5 shows that the drift-feeding parameters produce the possibility of all but the smallest trout having positive growth at night during summer, but that growth is much lower than during daytime. Exploration with the spreadsheet showed that night growth is very sensitive to *fishReactDistNightFactor*, much more so than to the parameters for drift concentration or energy content. When *fishReactDistNightFactor* has a value of 0.4, for example, there is no positive growth for fish of any length at any velocity. For search feeding (Figure A.6), only small trout at low velocities (bottom left corner) experience positive growth, but this is true in daytime as well as night. Darkness reduces the magnitude of growth and slightly reduces the range of fish sizes and velocities at which growth is positive. This result is within expectations.

A.

B.
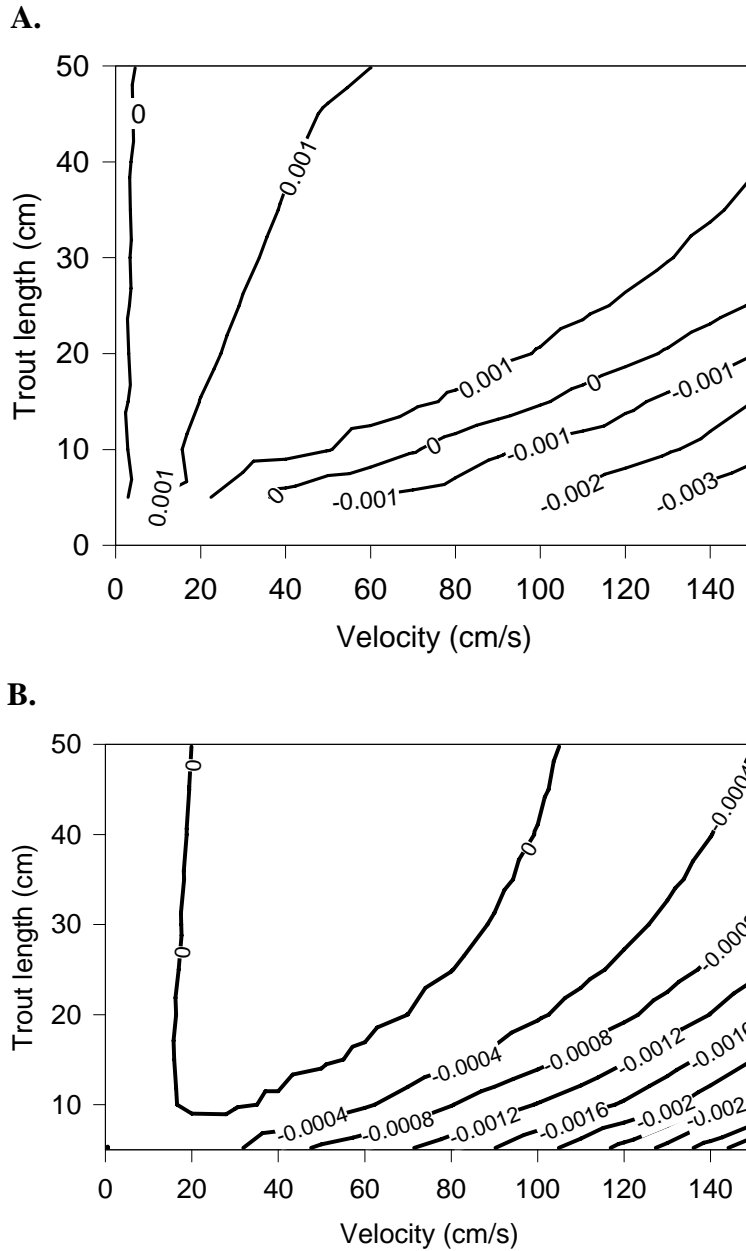
FIGURE A.5 Relative Growth (g/g/h) for Drift Feeding at 12ºC, during (A) Daytime and (B) Night. Contours show growth for fish with lengths 5–50 cm, at velocities of 0–100 cm/s. Depth was 200 cm, turbidity was negligible, and fish were using velocity shelter. Note different scales between A and B.

A.

B.
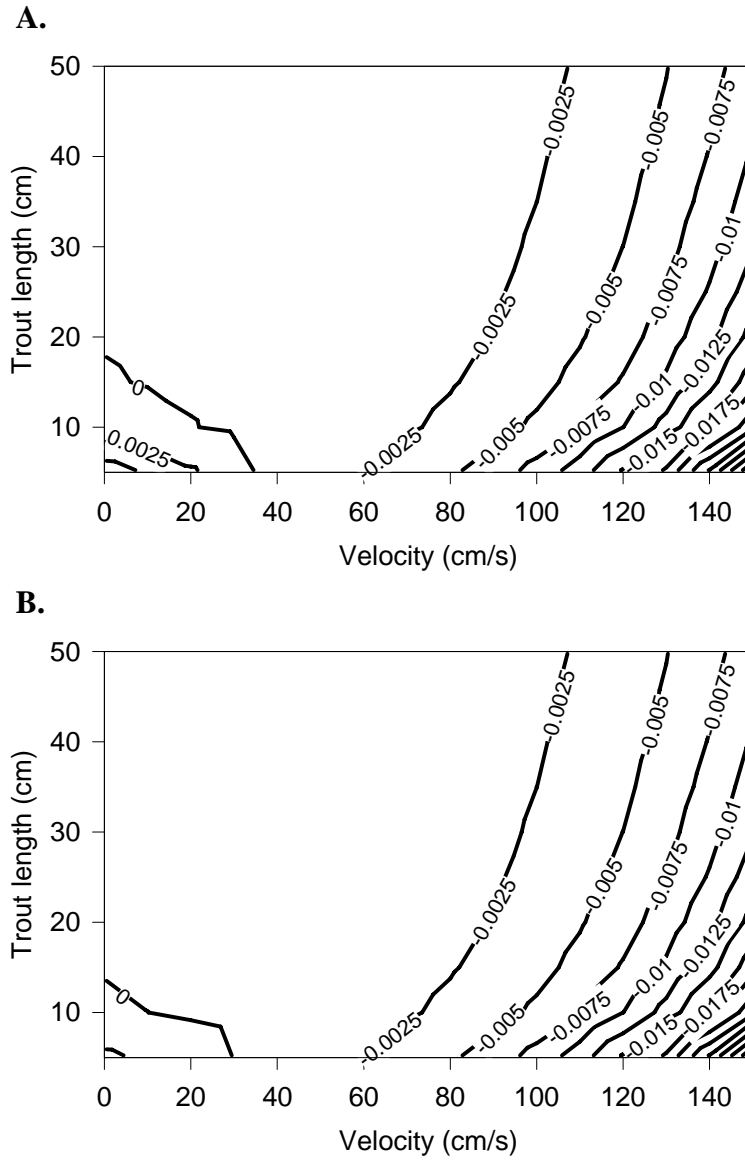
FIGURE A.6 Relative Growth (g/g/h) for Search Feeding at 12ºC, during (A) Daytime and (B) Night. Format and assumptions are the same as Figure A.5.

A.4.2 TEST VERSION OF MODEL

To facilitate calibration and validation of the trout IBM, a reduced version of the model and input was assembled. This version was designed to make simulations less complex, so that it is easier to test the components of greatest concern (especially, habitat and activity selection), and to execute faster, so more and longer test runs can be completed. The model was simplified by turning off the simulation of spawning and angling mortality. Input was reduced and simplified by:

- Using habitat data for the Pipe Creek site, but using only 10 transects. The input was developed from PHABSIM data that had 10 transects (Section A.3.3); the reduced input set used only one copy of each of the 10 transects. (Transects 1, 3, 6, 10, 13, 14, 17, 20, 23, and 25 of the full input were retained.)

- Reducing the transect length (cell length in the upstream-downstream direction) to 3 m.

- Simulating a fictitious ten-year period of October 1, 2005 to September 30, 2015.

- Assuming flows are steady at 60 m3/s (approximately the long-term average base flow).

- Using temperature data observed in the tailrace section from January 1, 2001, to December 31, 2001. This year of data was used for all 10 years of the test input set.

- Using an initial trout abundance 10% of that for the full Pipe Creek site; the full site is 482 m long and the test input reach is 30 m long. However, only rainbow trout were included.

- Assuming 100 rainbow trout are stocked each year in mid-May.

A.4.3 TEST FOR GENERAL PATTERNS OF 'REASONABLENESS' OVER MULTI-YEAR SIMULATIONS

The next calibration step was to test the trout IBM for any clearly unreasonable behaviors in long-term simulations. We defined several general patterns of population behavior that, if not reproduced by the IBM, would indicate problems needing to be resolved before calibration continued. These patterns are:

- Continued growth of adults. Adult trout must continue to grow after reaching the minimum size for spawning (Section A.2.5).

- No severe reduction in abundance. Our revised fitness measure encourages adult trout to continue growing, which inevitably incurs a penalty of increased mortality risk (compared to the alternative of feeding less and hiding more). However, we do not expect continued growth to come at such a cost that trout abundance is severely reduced. We have no clear basis for a criterion, but decided that a reduction of abundance by more than 5–10%, compared to simulations in which adults have no incentive to grow, would be a concern (Section A.2.5).

- Stable size distribution. The mean size of an age class must not exhibit trends over many years. Especially, the oldest age class (3 years and older) must not continue to get larger and larger over years. This is a concern because the "expected length" fitness function is based on the length of the largest fish in the population—the smaller a fish is in comparison to the largest fish, the more incentive it has to grow.

- Some feeding during both daytime and nighttime. Before testing whether diel patterns of feeding and activity vary as expected with various conditions, we simply ensure that fish are not "locked into" daytime or nighttime feeding.

The test version of the model was run for 10 years to test these patterns. Results were archived and are discussed only generally here.

One result from the test simulations is that it takes over a year for the IBM to develop its own patterns of abundance, size, and diel activity that are independent of the initial conditions. For example, after the first year, the size of age 1 and 2 trout appear strongly affected by the size of stocked trout, not by the size of the initial population. Age 3+ trout grew rapidly in the first year before their mean size stabilized.

The first test pattern, continued adult growth, was clearly met. All age classes continued to grow throughout the year, although winter growth was lower than summer growth. This growth is indicated by the graphs of mean length and weight of each age class.

The second pattern, abundance not severely reduced, was tested by comparing abundance results to those from a second simulation in which growth above the minimum size of spawning was assumed to provide no fitness benefit (so model adult trout had no incentive to grow). This second simulation was run for only 5 years. The 3+ age class was used for comparison because its abundance is less controlled by the stocking rate. We found that mean abundance of this age class, over simulation years 3 to 5, was very similar with and without the fitness function encouraging growth. Therefore, the fitness measure promoting growth of adults appears to cause very little additional loss of abundance.

The third test pattern, stable size distributions, was met. During the first simulation year the mean size of age 1 and 2 trout decreased because the size used to initialize the simulation was greater than that resulting from simulated initial size and growth of stocked trout. In contrast,

age 3+ trout grew rapidly during the first year, and their mean length stabilized at a value about 50% higher than that of the initial population.

The fourth pattern was also met. For all age classes, there was feeding during both daytime and nighttime at all times of year.

Some additional test simulations were run to develop a relationship between the "expected length" fitness function (Section A.2.5) and growth. These simulations are described in Table A.11.

This comparison of "expected length" functions shows several interesting points. As expected, the function with strongest growth incentive (Function 4) results in the largest trout. However, the function with no growth incentive for trout >25 cm (1) also produces growth comparable to that resulting from the other functions. The function with the smallest non-zero growth incentive (2) produced the smallest fish. The fact that Function 2 produced smaller age 3 trout than did Function 1 is explained by Function 1 providing a much stronger incentive for younger fish to grow toward spawning size rapidly (many age 2 fish are less than the spawning size of 25 cm). (For Function 1, the mean age 2 length is 29.5 cm; for Function 2, age 2 fish average 27.6 cm over the first 5 simulation years.) The mean abundance values in Table A.11 may not be meaningful compared to the stochasticity we typically see in the IBM's abundance results, but they do indicate the expected negative relationship between abundance and growth.

The observation that adult trout grew steadily even with the expected length function providing no fitness benefit to additional growth contradicts earlier observations from the IBM. The growth observed in these simulations could be an artifact of the small habitat size simulated—with only a small number of habitat cells to choose from, trout may have been less able to maximize survival to the point that no growth occurs. We tested this possibility by running a short simulation with the small test population in the full Pipe Creek habitat model, using Function 1, which provides no growth incentive for adults. Results for simulated individual adult fish were followed to see if they grew or spent more time hiding and avoided growth (directory TestInput-flatfitness3-BigHab). This experiment indicated that even with many habitat choices, adult fish continued to grow rapidly.

TABLE A.11 Calibration Analysis of "Expected Length" Fitness Function Effects on Growth

Function (experiment name)	Fitness Value for Expected Length = Minimum Spawning Length	Fitness Value for Expected Length = Length of Largest Fish	Mean Length of Age 3 Trout over Simulation Years 1–5 (cm)	Mean Abundance of Age 3 Trout over Simulation Years 1–5
1 (TestInput-flatfitness3)	0.8	0.8*	54.1	200
2 (TestInput-flatfitness2)	0.995	0.99999	53.4	211
3 (TestInput-flatfitness)	0.99	0.9999	54.1	203
4 (TestInput)	0.8	0.95	56.1	196

*   For expected length less than minimum spawning length, the fitness function follows the same logistic curve as in scenario 4; for expected length greater than minimum spawning length, the fitness function remains at 0.8.

Tracking the status of individual simulated fish in this experiment also indicated that there was little difference in survival probability between hiding and feeding activities, and in fact feeding sometimes offered higher survival probability than hiding—certainly an important explanation for why fish continued to grow even when not given a fitness incentive. Survival probability appeared to be sometimes higher for feeding than hiding for two reasons. First, the initial value of the parameter *mortFishTerrPredCoverFactor* was 0.95 (Section A.2.4.2), so a hiding fish still has 5% of the predation risk of an active fish, all else being equal. Second, the initial parameters for the terrestrial predation risk reduction functions for depth and velocity provided very high protection from predation at depths above about 3 m and velocities above 1.5 m/s—both of which are common in the Green River sites. However, otters (among the dominant predators) still pose a significant risk at high depths and velocities. Therefore, our initial parameters were unrealistically protecting trout feeding in high depths and moderate velocities from predation risk. These problems were corrected by making the following changes in parameter values:

- *mortFishTerrPredCoverFactor* changed from 0.95 to 0.99

- *mortFishTerrPredD1* unchanged at 50 cm

- *mortFishTerrPredD9* changed from 300 to 1,000 cm

- *mortFishTerrPredV1* unchanged at 20 cm/s

- *mortFishTerrPredV9* changed from 100 to 300 cm/s

These parameters were tested in two simulations, one using expected length Function 1 (no growth incentive for adults; experiment TestInput-flatfitness3-RevPred) and one using expected length Function 3 (reduced incentive for adults to grow; experiment TestInput-flatfitness2-RevPred). In both cases, the mean size of adults continued to increase in summer, but mean size decreased over years. Age 3+ trout fed little in daytime, and abundance was low compared to previous simulations. These simulations indicate that the changes in terrestrial predation risk parameters had two undesirable consequences: they apparently changed the risk landscape sufficiently to cause a major drop in abundance over the first several years, and almost completely eliminated daytime feeding by age 3+ trout.

During the preceding calibration simulations, we observed that starvation mortality was very high compared to previous versions of the trout IBM—for example, the number of age 3+ trout succumbing to starvation mortality was up to 70% of terrestrial predation mortality, which normally dominates. Starvation mortality was high because when fish hide, their condition factor declines slightly, placing them at risk of starvation. The high starvation mortality may not adversely affect model dynamics (starvation and predation parallel each other because fish make decisions to balance these two risks), but makes model results look unrealistic. We tried an experiment with two simulations to avoid this problem. The first simulation changed the parameters for starvation survival so that survival declines much less rapidly as condition decreases. Parameter *mortFishConditionK1* was changed from 0.3 to 0.2, and *mortFishConditionK9* was changed from 0.6 to 0.5, producing the survival function in

Figure A.7. With this new function, survival of starvation for 30 days is 0.9978 when K is 1.0, 0.96 when K is 0.8, and 0.47 when K is 0.6. (The condition factor K is the ratio of fish weight to the weight of a "healthy" fish of the same length.)

The first simulation (RevStarv_FlatFitness3) included no fitness incentive for adults to continue growing. This simulation was expected to produce very little growth in adults and still produce relatively high starvation, as adult trout still find a balance between predation risk and starvation risk, but this balance occurs at lower values of K. This simulation did indeed produce lower (but not zero) growth in adults, and starvation that was still high compared to previous versions of the IBM (but lower than in the previous calibration runs of this version).

In the second simulation of this experiment, the original expected length fitness function (Function 4 in Table A.11) was added back to the model. This simulation (experiment RevStarv_TestInput) was predicted to produce continued growth by adults but little starvation—the expected length function should encourage trout to grow, keeping their K value above the range where starvation mortality is likely. This simulation produced lower starvation mortality—approximately 30% of terrestrial predation mortality for age 3 and older trout. However, this simulation also produced long-term declines in trout size.

Finally, we experimented with steeper "expected length" fitness functions. The best (experiment RevStarv_ModFitness) uses a fitness value of 0.7 when expected length is equal to minimum spawning length and 0.9 when expected length is the length of the largest fish. For comparison to other versions in Table A.11, this function produced a mean length, over the first five simulation years, of age 3 trout of 38.6 cm (which is much more realistic, the observed mean length used to initialize the IBM being 37 cm); and a mean age 3 abundance of 217. The mean
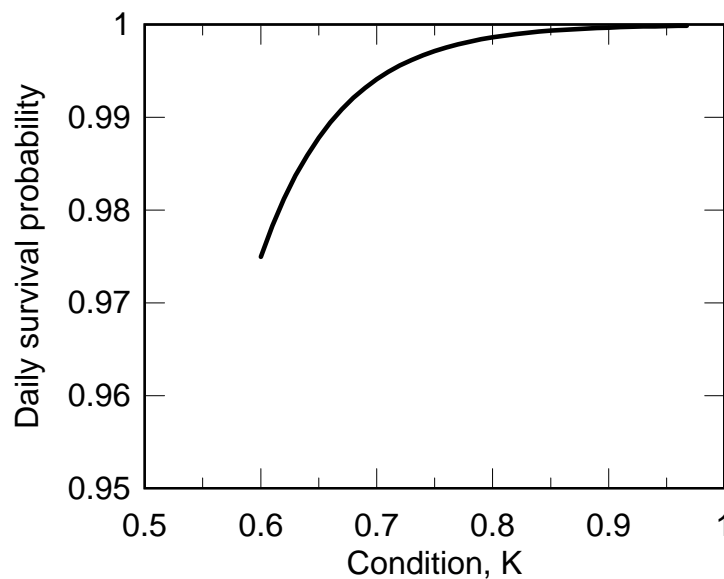

FIGURE A.7 Revised Starvation Survival Function

age 3 abundance actually increased over the first six years and stabilized in the last four at around 250. Starvation mortality still was prominent, but much less than in the initial calibration (29% of terrestrial predation mortality).

This comparison of "expected length" functions shows several interesting points. As expected, the function with strongest growth incentive (Function 4) results in the largest trout. However, the function with no growth incentive for trout >25 cm (1) also produces growth comparable to that resulting from the other functions. The function with the smallest non-zero growth incentive (2) produced the smallest fish. The fact that Function 2 produced smaller age 3 trout than did Function 1 is explained by Function 1 providing a much stronger incentive for younger fish to grow toward spawning size rapidly (many age 2 fish are less than the spawning size of 25 cm). (For Function 1, the mean age 2 length is 29.5 cm; for Function 2, age 2 fish average 27.6 cm over the first 5 simulation years.) The mean abundance values in Table A.11 may not be meaningful compared to the stochasticity we typically see in the IBM's abundance results, but they do indicate the expected negative relationship between abundance and growth.

The observation that adult trout grew steadily even with the expected length function providing no fitness benefit to additional growth contradicts earlier observations from the IBM. The growth observed in these simulations could be an artifact of the small habitat size simulated—with only a small number of habitat cells to choose from, trout may have been less able to maximize survival to the point that no growth occurs. We tested this possibility by running a short simulation with the small test population in the full Pipe Creek habitat model, using Function 1, which provides no growth incentive for adults. The status of individual simulated adult fish were tracked to see if they grew or spent more time hiding and avoided growth (directory TestInput-flatfitness3-BigHab). This experiment indicated that even with many habitat choices, adult fish continued to grow rapidly.

This best version met the four test patterns defined above. Trout continued to grow after reaching minimum spawning size, though at a much lower rate than juveniles. This growth did not come at a severe penalty in abundance. The 10-year mean abundance of age 3 trout was 233. For comparison, the otherwise identical simulation using the original fitness function (0.8, 0.95 at the two length landmarks) produced a 10-year average age 3 abundance of 253 (while also producing a steady decline in mean size). The size distribution of each age class was stable over years: mean length declined over the first half of the simulation but then stabilized. The maximum length increased only 1–2 cm over the entire 10-year simulation. Finally, all age classes exhibited both day and night feeding.

Several other interesting patterns were exhibited by this best version of the IBM. First, there were strong, yet complex, seasonal patterns in diel activity that were very consistent from year to year, indicating that they were driven mainly by temperature. (The same 365-day temperature record was used for all simulation years.) Second, these simulations produced a realistic pattern not previously exhibited by the trout IBM: fish on average lost weight in winter. Also, starvation mortality was higher in winter than in summer, whereas predation mortality was lower in winter and higher in summer; previously, these two kinds of mortality paralleled each other closely. Finally, the largest trout grew very little yet appeared to live for many years.

**A.4.4 TESTS OF *INSTREAM-SD*'S THEORY FOR HABITAT
         AND ACTIVITY SELECTION**

The final calibration and testing step was testing whether the model could reproduce a wide variety of patterns, observed in real salmonids, that emerge from how habitat and activity selection are modeled (Section A.2.1.4). This test used a series of simulation experiments, each reproducing the conditions under which a particular pattern has been observed and then verifying that the model could reproduce the pattern. These experiments were documented in the journal article by Railsback et al. (2005).

A.5 DETAILS OF MEMORY APPROACH TO
HABITAT AND ACTIVITY SELECTION

This section provides a detailed description of how *inSTREAM-SD* models habitat and activity selection by trout. The overall approach was described in Section A.2.1.4.

A.5.1 MEMORY VARIABLES

Of the approaches for modeling how fish move considering diel differences in expected growth and survival, we chose the "memory approach" to implement (Section A.2.1.4). The following steps are followed in implementing this approach.

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

- *netEnergyForFeedingLastPhase* is the hourly net energy intake rate (j/h) that the fish experienced while feeding during the previous phase, *or* the net energy intake the fish would have experienced had it chosen to feed in the best cell for feeding;

- *survivalForFeedingLastPhase* is the daily survival probability that the fish experienced while feeding during the previous phase, *or* the survival rate the fish would have experienced had it chosen to feed in the best cell for feeding;

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

- *survivalForHidingLastPhase* is the daily survival probability that the fish experienced while hiding during the previous phase, *or* the survival rate the fish would have experienced had it chosen to hide in the best cell for hiding.

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

A.5.2 MOVEMENT DECISION

The movement calculations use the following steps, whether movement is conducted at the start of a day or night phase, or because the flow changed. As with previous model versions, these steps are conducted by each fish, in order from largest to smallest fish. Each fish generates a list of potential movement destination cells, using the same method as the Version 2 cutthroat trout model. The potential destinations are then each evaluated using these steps:

- The fish determines whether it would have access to hiding cover if it chose to hide in the cell, using the approach described in Section A.2.4.1. The variable *isHideCoverAvailable* is set to YES or NO accordingly.

- The fish calculates the hourly net energy intake rate it would obtain if it fed in the cell (*hourlyNetEnergyIfFeed*, j/h). This rate is calculated using the existing feeding and bioenergetics methods, which includes determining whether the fish uses the search or drift feeding strategies. However, the energy intake methods are modified from previous versions to include the effect of night on food intake rates: if it is night, then food intake is modified, as described in Section A.2.2.

- The fish calculates the net energy intake rate it would obtain if it hid in the cell (*hourlyNetEnergyIfHide*, j/h). This rate, which will always be negative, is also calculated using the existing feeding and bioenergetics models with the following assumptions: Food intake is zero. The feeding strategy is set to "HIDE" (we have two fish variables, *cellFeedingStrategy* and *fishFeedingStrategy*, which can be set to 0 or 1 for DRIFT and SEARCH; we add a third value, –1 or HIDE). The respiration costs are calculated assuming a swim speed of zero (Section A.2.4.3).

- The fish calculates the daily non-starvation survival probability it would experience if it fed in the cell (*dailySurvivalIfFeed*, unitless). This probability is calculated as it is in previous versions of the model, except that survival probabilities depend on whether it is day or night (Section A.2.3). The survival probability assumes the fish is feeding, not hiding in cover (Section A.2.4.2).

- The fish calculates the daily non-starvation survival probability for hiding in the cell (*dailySurvivalIfHide*, unitless). This probability is calculated the same way as *dailySurvivalIfFeed*, except that some survival probabilities depend on the value of *isHideCoverAvailable*—if the fish has hiding cover available, then survival is increased (Section A.2.4.2).

- The fish calculates its Expected Reproductive Maturity in the cell for the four possible combinations of feeding and hiding. These calculations use one set of equations, and inputs to the equations that vary for the four combinations (and whether the current period is day or night). The inputs for each

combination are defined in Table A.12. Note that these calculations are based on the expected *daily* growth and survival, and do not depend on how many hours are actually in the model time step being simulated. They make use of day length variables defined in Section A.2.1.2.

The total daily net energy intake (*dailyNetEnergy*, j/d) is equal to:

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

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

$$[(survivalDay \times numberOfDaylightHours) + (survivalNight \times numberOfNightHours)]/24$$

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

TABLE A.12 Inputs for ERM Calculations

Current Phase	Daytime Activity	Night Activity	netEnergyDay	netEnergyNight	survivalDay	survivalNight
Day	FEED	HIDE	*hourlyNetEnergy IfFeed*	*netEnergyForHi dingLastPhase*	*dailySurvivalIfF eed*	*survivalForHiding LastPhase*
	FEED	FEED	*hourlyNetEnergy IfFeed*	*netEnergyForFe edingLastPhase*	*dailySurvivalIfF eed*	*survivalForFeeding LastPhase*
	HIDE	HIDE	*hourlyNetEnergy IfHide*	*netEnergyForHi dingLastPhase*	*dailySurvivalIf Hide*	*survivalForHiding LastPhase*
	HIDE	FEED	*hourlyNetEnergy IfHide*	*netEnergyForFe edingLastPhase*	*dailySurvivalIf Hide*	*survivalForFeeding LastPhase*
Night	FEED	HIDE	*netEnergyForFe edingLastPhase*	*hourlyNetEnergy IfHide*	*survivalForFee dingLastPhase*	*dailySurvivalIfHide*
	FEED	FEED	*netEnergyForFe edingLastPhase*	*hourlyNetEnergy IfFeed*	*survivalForFee dingLastPhase*	*dailySurvivalIfFeed*
	HIDE	HIDE	*netEnergyForHi dingLastPhase*	*hourlyNetEnergy IfHide*	*survivalForHidi ngLastPhase*	*dailySurvivalIfHide*
	HIDE	FEED	*netEnergyForHi dingLastPhase*	*hourlyNetEnergy IfFeed*	*survivalForHid eingLastPhase*	*dailySurvivalIfFeed*

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

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

A.5.3 UPDATE OF MEMORY VARIABLES

The memory variables are also updated during evaluation of each potential destination cell. How the memory variables are updated is very important to the movement calculations.

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

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

- At the start of movement actions, the fish determines whether movement is due to the start of a new phase or due to a flow change. If movement is due to a new phase, then the four memory variables are replaced by the values of the corresponding temporary memory variables. If movement is due to a flow change, then the memory variables are unchanged.

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

- If the current phase is daytime, the ERM for the daytime-feed, night-hide activity combination is compared to the value of *tempBestERMForFeed*. If the cell's ERM for this activity combination is greater than

tempBestERMForFeed, then the value of *hourlyNetEnergyIfFeed* for the cell replaces *tempNetEnergyIfFeed*, the value of *dailySurvivalIfFeed* for the cell replaces the current value of *tempSurvivalIfFeed*, and *tempBestERMForFeed* is replaced by the cell's ERM for this activity combination.

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

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

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

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

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

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

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

A.5.4 POTENTIAL FUTURE CHANGES

Two potential future changes were identified after the flow fluctuation experiments were completed. These changes have not been implemented because they are not particularly important compared to the value of documenting and archiving the model exactly as it was used in the flow fluctuation study.

Recently published research (Hughes et al. 2003) indicates that our reactive distance (the distance over which trout can detect and attempt to capture drifting prey) equations may not be accurate for trout as large as those in the Green River. The equations assume reactive distance increases rapidly with fish length, whereas the new literature indicates that reactive distance, a function of visual acuity and maneuverability, increases with size but not linearly at large sizes. The approach to modeling reactive distance was revised in Version 4 of *inSTREAM*, but throughout the calibration and validation (Section A.4) there was no indication that the approach used in *inSTREAM-SD* causes significant errors.

In preparing Version 4 of *inSTREAM*, an error was found in the scour function for redd mortality. (A coefficient in an equation for a scour parameter was inadvertently 0.33 instead of 3.33 in the documentation of Version 2 and in the software for Versions 2 and 3.) This error had no effect on Green River simulation experiments because spawning and redds were not simulated.

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