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An Individual-Based Instream Flow Model for Coexisting Populations of Brown and Rainbow Trout

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REPORT SUMMARY

An Individual-Based Instream Flow Model for Coexisting Populations of Brown and Rainbow Trout

A new brown and rainbow trout model incorporates physical, chemical, and biological factors believed to be important in determining fish population size and dynamics. This model will support more realistic predictions of fish population responses to flow changes than existing methods, which assume that only physical factors such as flow are important. As a result, the model will allow more realistic evaluation of instream flow scenarios and will increase the cost-effectiveness of instream flow recommendations.

INTEREST CATEGORIES

Land and water quality
Hydroelectric

KEYWORDS

Hydroelectric power
Instream flow
Population dynamics
Licensing
Environmental impact
Fish

BACKGROUND One of the most common issues of contention during relicensing of hydropower plants by the Federal Energy Regulatory Commission is instream flow. Because this water is not available for electricity generation, requirements for instream flows are costly to utilities. Many decisions about how much instream flow is needed have been based on the U.S. Fish & Wildlife's Instream Flow Incremental Methodology, which assumes that physical habitat alone (velocity, depth, substrate structure, cover, and occasionally temperature) determines fish population response to changes in flow. Methods that incorporate other potentially important determinants of fish population size are needed to ensure that instream flow needs do not encroach upon instream uses and cost-effective electricity production.

OBJECTIVE To develop an instream flow model that can incorporate changes in chemical and biological variables as well as physical habitat to predict instream flow needs where brown and rainbow trout are typically the primary coexisting fish species.

APPROACH Investigators developed an instream flow model for coexisting trout species by combining the hydraulic component of the Physical Habitat Simulation (PHABSIM) model, developed by the U.S. Fish & Wildlife Service, with an integrated brown and rainbow trout individual-based fish population model. They simulated physical stream habitat from a PHABSIM study, a mesohabitat study, and daily values for flow and temperature. Calculations of velocity and depth for each PHABSIM cell in each habitat unit are based on the daily flow. Population values are calculated by scaling up according to the proportion of model individuals sampled from the baseline population.

RESULTS This model—developed under EPRI's long-term program on Compensatory Mechanisms in Fish Populations (CompMech), with cosponsorship from Pacific Gas & Electric Company and Southern California Edison Company—represents the brown and rainbow trout life cycles by a series of linked subroutines that include formulations for spawning, development, and mortality of eggs and alevins in the redd as well as foraging, consumption, energetic costs, habitat use, movement, and mortality of individual trout from fry to adult.

Model development benefited immensely from two multiday workshops in 1992 and 1994 involving knowledgeable utility, agency, and academic scientists. The resulting model was applied to a stream segment in California's Tule River. Physical and biological data from this site were used as model input, and the model was calibrated for two water years.

Simulated trout length distributions were in excellent agreement with observed distributions for both water years, indicating that the coupling of an individual-based bioenergetics model with a simulated stream habitat can accurately simulate trout growth. Simulated abundances for one year were in reasonable agreement with observed abundances, although simultaneously matching observed abundances for three age classes of both trout species for both water years proved difficult. Simulated habitat suitability was in good agreement with observed use for both depth and focal velocity. The model is now ready for use in evaluating alternative temperature regimes and minimum instream flow regimes.

EPRI PERSPECTIVE The CompMech two-species brown and rainbow trout individual-based population model represents a significant improvement over the best alternative instream flow model. Inclusion of biological characteristics, interpopulation interactions, and physical habitat variables in the determination of the flows needed to maintain fish populations below dams leads to more accurate flow estimates. By using this model, utilities will be less likely to face requirements for increased instream flows that do not result in concomitant increases in fish. Related EPRI research includes *Applicability of the CompMech Trout Model to Hydropower Impact Assessment* (EPRI report TR-103028).

PROJECTS

RP2932-02; RP9046-02; RP9111-01
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Environment & Health Studies
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TR-106258
Research Projects 2932-02; 9046-02; 9111-01

Interim Report, March 1996

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ABSTRACT

This report describes an individual-based model for sympatric populations of brown and rainbow trout in a stream habitat. Hatchery rainbow trout are included as a third species. The model provides a tool for predicting flow effects on trout populations by linking the hydraulic component of the Physical Habitat Simulation (PHABSIM) methodology and an individual-based population modeling approach. PHABSIM simulates the spatial distribution of depth and velocity at different flows. The individual-based model simulates the reproduction, foraging, consumption, energetic costs, growth, habitat utilization, movement, and mortality of individual fish, and enables population attributes to be determined from relevant attributes of individual fish. The spatially explicit nature of the model permits evaluation of behavioral responses used by fish to mitigate temporary setbacks in habitat quality. This linked mechanistic modeling approach readily lends itself to the iterative process of making predictions, testing against field data, improving the model, and making more predictions. The model has been applied to a stream segment in the Tule River, California. Physical and biological data from this site are used as input to the model. Given initial model populations on October 1, parameters were adjusted until model predictions of population abundance, length, and habitat utilization on June 30 and September 30 of the following year were in reasonable agreement with observed estimates. We found that calibrating the model to abundance data was relatively easy because values for mortality parameters were not strongly constrained by empirical data. Calibrating the model to observed growth rates and habitat use was more challenging because values for most bioenergetic parameters were constrained by empirical data. The primary reason for developing this model has been to provide a new and complementary tool to PHABSIM that can be used in instream-flow assessments. The ongoing Response of Fish Populations to Altered Flows Project, sponsored by the Electric Power Research Institute, Pacific Gas & Electric Company, and Southern California Edison Company, and other studies have documented that factors other than those involved in a PHABSIM analysis of weighted useable area can limit trout populations. The model increases realism by focusing on physical habitat and the reproduction, growth, and mortality of individual fish.

ACKNOWLEDGMENTS

We gratefully acknowledge the input of numerous participants at two major workshops that were held during the development of this model (April 1992 and December 1994). A list of participants at the December 1994 workshop is included as Appendix 6. In calibrating the model to the Tule River site, we have relied heavily on Pacific Gas & Electric Company staff and their contractors, especially Jean Baldrige, Gene Geary, Steve Railsback, and Tom Studley. Libby Marschall, Rob McLaughlin, Ray Newman, David Noakes, Bob Otto, and Sam Williamson provided important input at various times during model development and the review of this report. Finally, we acknowledge the long-term institutional commitment to this project and the Altered Flows Project by the Electric Power Research Institute (Jack Mattice), Pacific Gas and Electric Company (Donna Lindquist and Ellen Yeoman), and Southern California Edison (John Palmer). This research is sponsored by the Electric Power Research Institute under contracts RP2932-2, 9046, and 9111 (DOE number ERD-87-672) with the U. S. Department of Energy, under contract DE-AC05-84OR21400 with Lockheed Martin Energy Systems, Inc. This is Publication No. 4474 of the Environmental Sciences Division, Oak Ridge National Laboratory.

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EXECUTIVE SUMMARY

This report describes an individual-based model for sympatric populations of brown and rainbow trout in a stream habitat. Hatchery rainbow trout are included as a third species. The model provides a tool for predicting flow effects on trout populations by linking the hydraulic component of the Physical Habitat Simulation (PHABSIM) methodology and an individual-based population modeling approach. PHABSIM simulates the spatial distribution of depth and velocity at different flows. The individual-based model simulates the reproduction, foraging, consumption, energetic costs, growth, habitat utilization, movement, and mortality of individual fish, and enables population attributes to be determined from relevant attributes of individual fish. The spatially explicit nature of the model permits evaluation of behavioral responses used by fish to mitigate temporary setbacks in habitat quality. This linked mechanistic modeling approach readily lends itself to the iterative process of making predictions, testing against field data, improving the model, and making more predictions.

The goal in simulating the dynamics of the physical habitat of a stream is to capture those characteristics of real streams that are judged to be the primary determinants of the average daily dynamics of individual trout over a period of one or more years. To simulate the physical stream habitat, the model requires the following inputs: results from a PHABSIM study, a mesohabitat survey, and average values for flow and temperature for each day of the simulation. Velocity and depth as a function of flow are calculated daily for each PHABSIM cell in each habitat unit. A method is proposed for mapping cell depths, widths, and velocities in donor habitat units that have PHABSIM transects into cell depths, widths, and velocities in receptor habitat units that do not have PHABSIM transects. Field estimates at baseflow of the fraction of the area of a habitat unit with instream cover are assumed valid for all flows.

The life cycle of trout is represented in the model by a series of linked subroutines that include formulations for spawning, development and mortality of eggs and alevins in the redd, and foraging, consumption, energetic costs, habitat utilization, movement, and mortality of individual trout from fry to adult. A simulation can be started on any day of the year. However, it is logical to start simulations on one of the dates for which field data are available for the trout populations represented in the model. To simulate the trout populations, the model requires input for each species on trout density and length distribution for each year class.

The spawning module includes formulations for sexual maturity, timing and order of spawning, dependence of spawning on flow and change in flow, dependence of spawning on physiological condition, selection of a habitat unit and cell for spawning, and fecundity. As an example, selection of a habitat unit and cell for spawning is a function of the availability of suitable spawning substrate, water depth, and average water column velocity. Energetic costs are not considered in the representation of reproduction.

The module for development and mortality of eggs and alevins in the redd includes equations for the influence of female length on the length of fry upon emergence from a redd and for daily development rate as a function of temperature, which in turn controls the period of emergence of fry from each redd. The risks of mortality due to dewatering at low flow, scouring at high flow, low and high temperatures, and superimposition of one redd on top of an existing redd are represented separately.

The trout model is designed to link flow, microhabitat, and trout behavior to the daily growth of each trout. The bioenergetics model describing the daily growth of individual trout is Growth = Consumption − Energetic Costs. Foraging and consumption are represented in considerable detail in light of evidence that foraging success dominates the energetics of stream fishes. Space (i.e., feeding stations, cover), rather than prey, is treated as the contested resource. The spatially explicit nature of the model permits predicting habitat use and growth by relating drift rate, capture efficiency, and energetic costs to velocity. The individual-based nature of the model permits exploring the consequences of different behavioral strategies adopted by individual trout.

Each model trout is characterized each day as having a feeding station (stayer) or not (mover). Each day a trout forages either in the water column on drifting prey or near the stream bottom on benthic prey. Trout without a feeding station are required to feed on the benthos. For stayers, a rate of prey consumption for both drift and benthic foraging is calculated, and trout are allowed to feed in the mode that provides the higher consumption rate. Daily consumption is calculated by multiplying consumption rate by the time spent foraging. Daily consumption is constrained by the time available for feeding or the maximum quantity of prey the trout can digest in a day. Energetic costs and mortality risks are higher when a model trout is foraging. A nonforaging option is included that is helpful in calibrating and debugging the model and that provides a means of easily evaluating the response of trout to starvation and ad libitum feeding.

The term in the growth equation for energetic costs includes egestion, excretion, specific dynamic action, and standard and activity respiration. The lower temperature threshold imposed on foraging also applies to activity respiration. A new weight is calculated each day for each trout. On the basis of this weight, the length of the trout is updated and a new condition factor is calculated.

The module on habitat utilization and movement includes four reasons a model trout might move from its current cell and habitat unit and how a new location is selected. Each trout is given the opportunity to move each day. A trout may move if the ratio of mortality risk to growth is greater than expected, the PHABSIM cell is too shallow or its velocity is too high, the trout does not have access to a feeding station, or the trout does not have access to cover. The algorithms for selecting a new location involve evaluating adjacent cells and habitat units until a place is found that is physically habitable and not inaccessible to the trout because of an impassable cascade.

The module on mortality includes formulations for daily risk of mortality due to high temperature, high velocity (i.e., being swept downstream), spawning, and a composite function including factors for physiological condition, length of the trout, and time spent foraging. Fishing mortality is represented in considerable detail because it is a potential major source of mortality for Age 1 and older trout, data are commonly available to parameterize the equation, and fishing mortality is probably density dependent. A maximum daily probability of fishing mortality is specified, corresponding to conditions that would maximize the number of trout killed by anglers. This maximum is adjusted with a series of independent multipliers to incorporate the effects of density of trout; differences in vulnerability among brown trout, rainbow trout, and hatchery rainbow trout; day of the week; month of the fishing season; whether the trout is kept; and hooking mortality if the trout is released. Mortality of hatchery rainbow trout is handled separately in a more simplistic manner.

The model has been applied to a stream segment in the Tule River, California. Physical and biological data from this site are used as input to the model. The model has been calibrated for Water Years 1988 and 1991. Given initial model populations on October 1, parameters were adjusted until model predictions of population abundance, length, and habitat utilization on June 30 and September 30 of the following year were in reasonable agreement with observed estimates. We found that calibrating the model to abundance data was relatively easy because values for mortality parameters were not strongly constrained by empirical data. Calibrating the model to observed growth rates and habitat use was more challenging because values for most bioenergetic parameters were constrained by empirical data.

The primary reason for developing this model has been to provide a new and complementary tool to PHABSIM that can be used in instream-flow assessments. The ongoing Response of Fish Populations to Altered Flows Project, sponsored by the Electric Power Research Institute, Pacific Gas & Electric Company, and Southern California Edison Company, and other studies have documented that factors other than those involved in a PHABSIM analysis of weighted useable area can limit trout populations. The model increases realism (compared to PHABSIM) by focusing on physical habitat *and* the reproduction, growth, and mortality of individual fish.

A tradeoff does exist, however, because increased complexity accompanies the increased realism. Training in the application of the model is necessary. Some types of fisheries data not needed for a PHABSIM analysis are required. The tool is probably not appropriate for scoping-level, instream-flow assessments, whereas it is an ideal tool for any multiyear applied research studies involving the iterative cycle of study design, execution, analysis, interpretation, and prediction. The Altered Flows Project, funded by the Electric Power Research Institute, Pacific Gas & Electric Co., and Southern California Edison Co., is an example of such a study. Between these two extremes are in-stream flow assessments pitting water for fish against water for other uses such as hydropower and irrigation, where much more money is at stake than the incremental cost of applying this model. PG&E and SCE are evaluating the appropriateness of this model for such sites and as a framework for monitoring programs.

SECTION 1 INTRODUCTION

1.1 Project Objectives

In 1985, Pacific Gas & Electric Company (PG&E), Southern California Edison Company (SCE), and the Electric Power Research Institute (EPRI) initiated a multiyear study entitled Response of Fish Populations to Altered Flows Project (Altered Flows Project) (Studley et al. 1995). The goal of this ongoing project is to determine if fish populations respond to changes in minimum instream flows in a predictable manner. The Altered Flows Project is designed to (1) investigate assumptions and predictive capabilities of the weighted-usable-area (WUA) index for fish habitat (Milhous et al. 1989) and (2) evaluate limiting factors (e.g., fishing mortality, food availability) not commonly considered in applications of the U.S. Fish and Wildlife Servicess Physical Habitat Simulation methodology (PHABSIM).

In 1987, EPRI initiated a long-term program on Compensatory Mechanisms in Fish Populations (CompMech). The goal of this program is to develop improved simulation models to predict the effects of anthropogenic disturbances on fish populations and to evaluate the potential that fish populations possess for self-mitigating (i.e., compensating) for increased mortality and decreased growth and fecundity. We have addressed this goal by developing process-oriented, individual-based models for fish species representing a range of life history strategies (Winemiller and Rose 1992). Empirical studies at specific sites have contributed to model development and parameterization, and they provide the data required to test subsequent model predictions.

In 1992, EPRI, PG&E, and SCE agreed to jointly fund a project that is complementary to both the Altered Flows Project and the CompMech Program. The objectives of this joint project are to:

(1) develop a model that links the contemporary PHABSIM methodology with an individual-based model for sympatric brown and rainbow trout populations,

(2) contribute to the design of the Altered Flows Project in support of testing the model, and

(3) apply the model to other PG&E or SCE hydro sites to demonstrate its ability to predict effects of altered flow and temperature regimes on trout populations.

1.2 Report Objectives

One goal of this brown trout–rainbow trout model has been to provide an alternative to relying on habitat suitability indices (Studley et al 1995, Appendix D; EA Engineering, Science, and Technology 1994), in particular, an alternative that is more mechanistically based on the physiology, behavior, and ecology of trout than habitat suitability indices. Habitat suitability indices are required in PHABSIM applications to estimate weighted usable area (Fig. 1-1). Several studies have demonstrated, however, that the results of such applications are more sensitive to the habitat suitability indices than to the representation of the physical habitat (Armour and Taylor 1991; EA Engineering, Science, and Technology 1994; Mathur et al. 1985; Orth 1987). Unfortunately, while uncertainities in habitat suitability indices are widely acknowledged, the underlying causes of these uncertainties are poorly understood.

Our approach has been to represent the processes that underlie habitat utilization and to focus on the response variables of primary importance for characterizing the dynamics of brown and rainbow trout– namely, reproduction, growth, and survival (Figs. 1-1, 1-2). One of the secondary benefits of our spatially explicit approach is that it predicts habitat use by species, life stage, and season in terms of mesohabitat (e.g., pool, pocket water, riffle) and microhabitat (e.g., depth, velocity, substrate, cover). Thus, we can compare observed and predicted habitat utilization. We have included hatchery rainbow trout as a third species because they are commonly stocked in streams where this model might be applied. To some extent, they must compete for space and prey with the brown and native rainbow trout. As a result, they can potentially alter the spatial distribution, growth, and mortality of the brown and native rainbow trout.

Fig. 1-1 Individual-based models like the one described in this report complement and extend the PHABSIM methodology and other instream flow models in terms of components of a stream ecosystem that are represented.

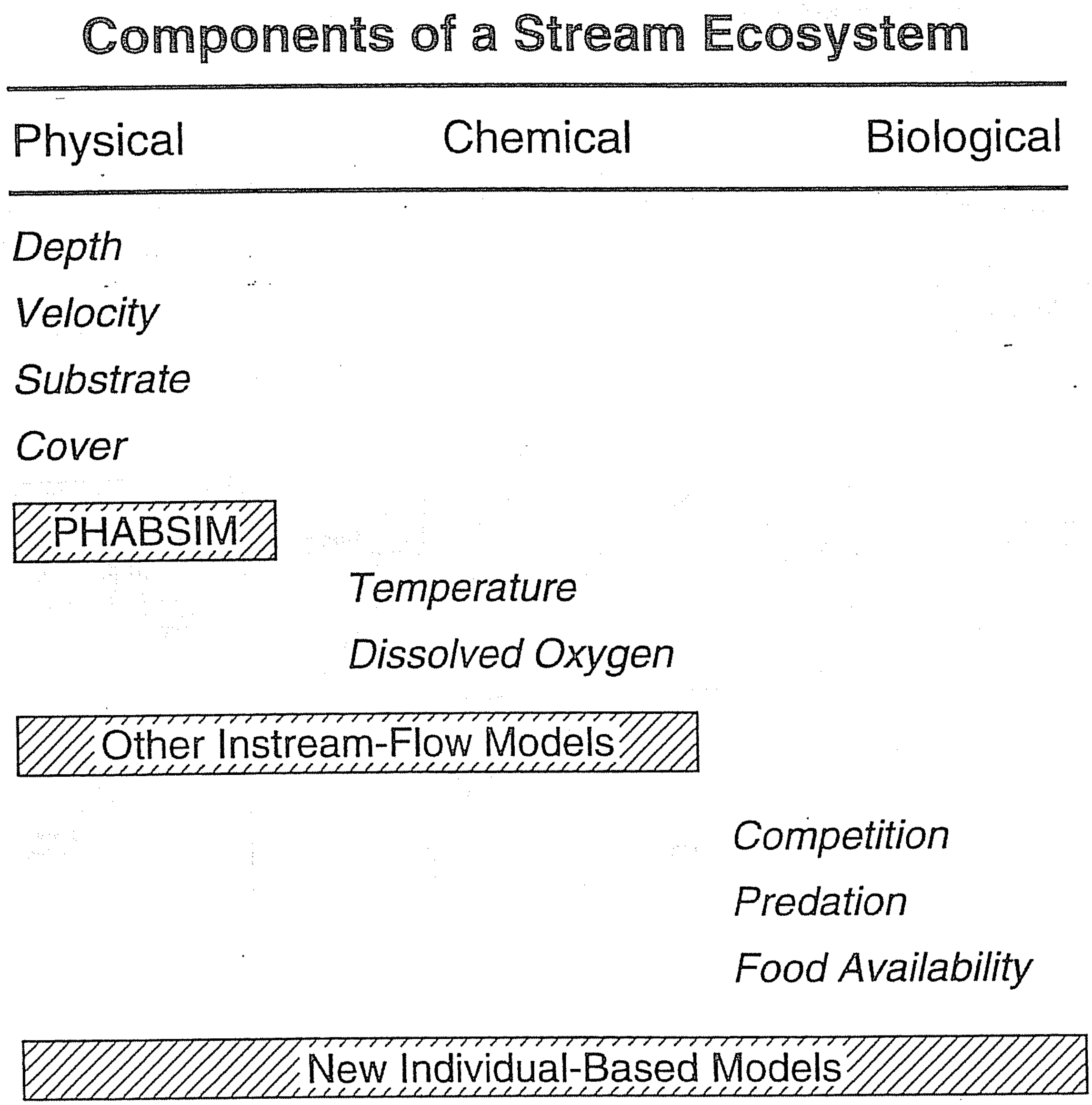
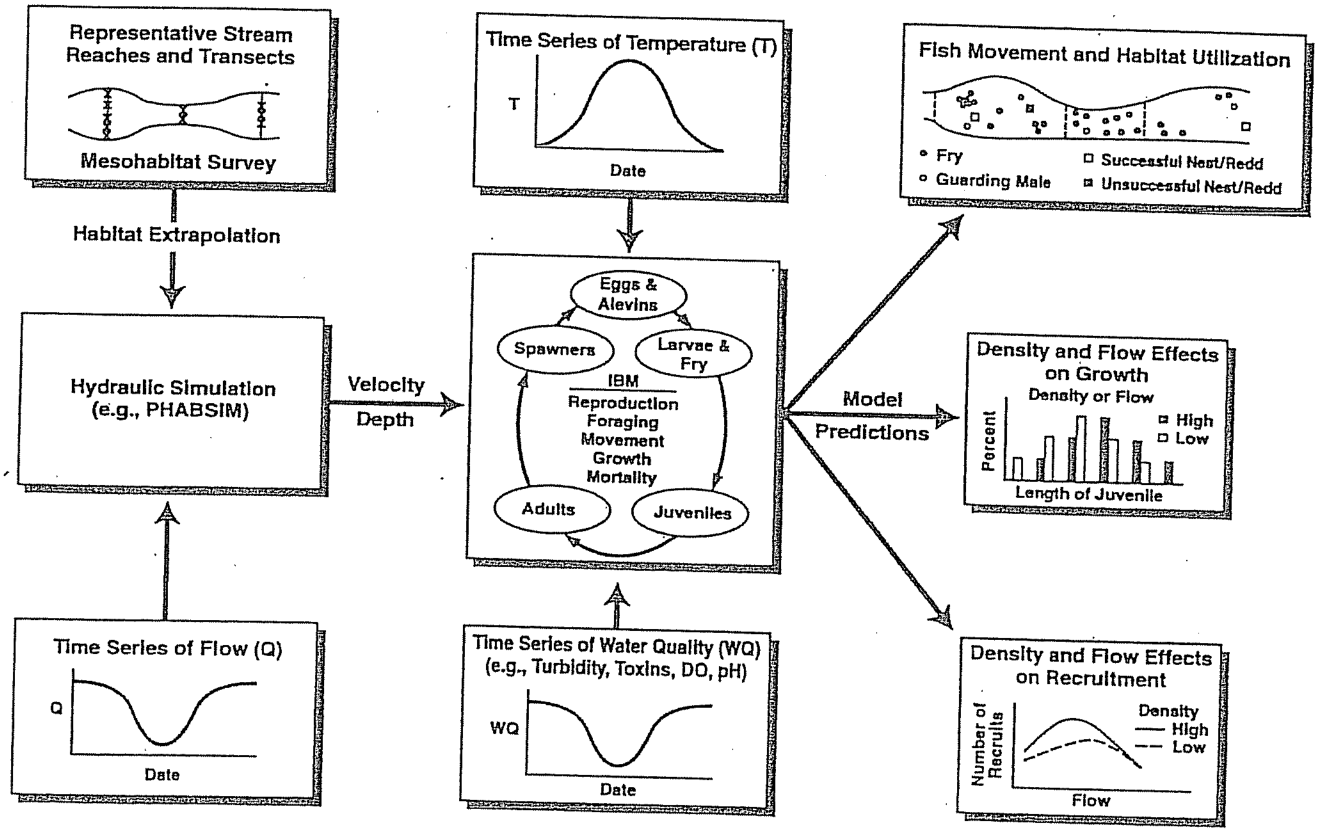


Fig. 1-2 Schematic of the model for sympatric populations of brown and rainbow trout illustrating links between (a) characterization of the physical habitat and (b) an individual-based model representing the different life stages and processes underlying reproduction, growth, and mortality. The model is a tool for evaluating the effects of alternative flow and temperature regimes based on measurable responses such as habitat use, growth, abundance, and recruitment.



In developing our model, we drew on the extensive scientific literature for salmonids. We paid particular attention to the following issues: (1) evidence concerning the effects of flow and temperature; (2) evidence that processes underlying reproduction, growth, and survival vary with trout density; (3) evidence supporting differences and interactions between the two species; (4) availability of data for calibration and validation; and (5) processes in need of further study.

The model covers the complete life cycle of a trout. The egg stage begins when fertilized eggs are placed in a redd and ends at hatching. Allan and Ritter (1977) define the end of the alevin life stage as the end of dependence on the yolk sac as the primary source of energy, which can occur before or after emergence from the redd. Elliott (1984a) notes that determining the end of the alevin stage according to the Allan and Ritter (1977) definition is difficult because the young trout may start feeding on invertebrates before all the yolk has been absorbed. In our model, the alevin life stage begins at hatching and ends at emergence from the redd. Individual redds are followed in the model rather than individual eggs and alevins. On the day of emergence an alevin is reclassified as a fry, which we assume has no yolk reserves and is capable of feeding; it is then followed in the model as an individual. A trout is reclassified from fry to juvenile when it attains a length of 50 mm—the length threshold commonly used in field studies dealing with habitat suitability of Age 0 trout. We do not consider fry and juveniles to be physiologically or behaviorally distinct life stages in terms of parameter values for any of our functions. On each January 1 in the model, juvenile brown and rainbow trout are reclassified: Age 0 trout become Age 1 trout, Age 1 become Age 2, etc.

Site-specific data required to run this simulation model are fairly modest. Daily time series of average flow and temperature values are needed as driving variables. Results from a PHABSIM study and a mesohabitat survey are needed to spatially represent the physical stream habitat. Results from a trout population survey are needed to characterize the initial densities and lengths of trout by year class for each species.

This report is intended for a mixed audience, and as such it involves some compromises. The level of detail and complexity will be higher than needed for most fishery managers and regulators. On the other hand, the level of detail, complexity, and documentation from the published literature will be less than wanted by some researchers. The report is organized as follows. We describe an approach for representing the physical habitat of a stream segment in Sect. 2. We describe our model formulations for spawning, development and mortality in the redd, foraging and consumption, energetic costs and growth, habitat utilization and movement, and mortality for brown and rainbow trout inhabiting a stream similar to the Tule River in Sects. 3–8. We describe model calibration and present results of comparisons of observed and predicted values for abundance, growth, and habitat use in Sect. 9. We discuss the tradeoff between increasing realism versus complexity in terms of research needs and the applicability of this model for improving instream flow assessments in Sect. 10.

Included in this report is a list of input parameters (Appendix 1), a description of the life history of brown and rainbow trout (Appendix 2), and a description of PG&Es study area in the Tule River, California (Appendix 3). MathCad files illustrating many of the equations used in the model are included in Appendix 4; an asterisk after the equation number in the text indicates that there is a MathCad worksheet for that equation in Appendix 4. Finally, Appendix 5 includes sample listings of input data files.

SECTION 2 PHYSICAL HABITAT

Our goal in simulating the physical habitat of a stream is to capture those characteristics of a real stream judged to be the primary determinants of the *average*, *daily* bioenergetics and behavior of individual brown and rainbow trout over a period of one or more years. Flow is the most fundamental physical habitat characteristic of a stream in that it influences so many other habitat variables known to be important to fish, such as water depth and velocity, type and amount of cover, water temperature, and prey availability. Inevitably the process of achieving this goal involves simplifications and approximations in representing both stream habitat and the biology and ecology of the trout.

The two principle driving variables of this model are average daily stream temperature and flow. Both can be simulated by a function ($I_{simQ} = 1$ simulates flow; $I_{simT} = 1$ simulates temperature), or provided by historical or hypothetical daily records. Flow simulation consists of specifying a constant value (Q_{set}). Temperature simulation generates a sinusoidal pattern of temperatures (average annual temperature = T_{ave} ; the first date when T_{ave} occurs = t_{Tave} ; maximum temperature = T_{max} ; see Jager et al. 1993). Files containing historical or hypothetical records of daily temperature and flow data can be provided as input with three columns each: year (e.g., 1993), julian day (e.g., 1–365), and temperature in units of °C or flow in units of cubic feet per second (cfs).

Habitat type (or mesohabitat) refers to the classification of stream habitats at the spatial scale of pools, runs, pocket waters, riffles, bedrock chutes, cascades, etc. (Bisson et al. 1982; Hawkins et al. 1993; Sullivan 1986). In our model, we reduce the types of mesohabitats to pool, run, pocket water, riffle, and impassable cascade. In our judgment, this level of distinguishing between habitat types is adequate for our purposes, although even at this level, differences between types start to blur over the full range of flows (Roper and Scarnecchia 1995). Habitat unit refers to a specific length of stream of a given habitat type.

The model requires two types of input to characterize the stream segment being modeled. The first is a mesohabitat map and data set of the entire segment represented in the model. The data set includes (1) the sequence of habitat types and (2) the length, mean width, mean depth, and substrate and cover characteristics for each habitat unit at a base or reference flow. In the case of the application presented in this report (i.e., Segment 8 of the North Fork Middle Fork Tule River in California), the stream segment is 1.1 km long and consists of 131 habitat units; see Appendix 5 for a mesohabitat map and a data input file giving the length, mean width, mean depth, and the cover and spawning substrate characteristics for each habitat unit at base flow). The second type of input information required for each of these habitat units is hydraulic data relating depth and velocity to flow at representative, cross-stream transects. These transects are chosen to be in habitat units representive of pool, run, pocket water, and riffle habitat types (Milhous et al. 1989). We have hydraulic data for 10 of the 131 habitat units in Segment 8 of the Tule River. We use a PHABSIM code that has been modified to create, from a standard PHABSIM input file, an input file containing estimates for the hydraulic parameters used in our trout model. This input file contains hydraulic parameter estimates for stations along each of the 10 cross-stream transects.

2.1 Depth and Velocity

An important function of our model is to produce a realistic streamscape with trout habitat (depth and velocity) that responds to streamflow. Because it is not feasible to measure the hydraulics of all habitat units in large sections of stream, we have developed a method of simulating the hydraulics of all habitat units from information contained in sampled PHABSIM transects. We assign each habitat unit that lacks hydraulic transect data (receptor habitat unit) a donor habitat unit with similar habitat type, mean depth, mean width, and percent cover. The donor units are those having hydraulic transect data. Model cells within each donor habitat unit are centered on sites where hydraulic data were collected and are expanded or contracted to fit the receptor units. The result is a two-dimensional grid of cells over the entire stream segment; each cell is typically less than a meter wide and extends the full length of a habitat unit.

The model simulates the depth and average water column velocity as a function of flow on a daily basis for cells in each pool, run, pocket water, and riffle (but not cascade) habitat unit (Jager et al. 1993). First we simulate the hydraulics of cells in donor habitat units and then tailor these estimates for receptor habitat units. We map depths, widths, and velocities from transect cells in donor habitat units into depths, widths, and velocities for cells in the receptor habitat units (Fig. 2-1).

Hydraulic simulation for donor cells is accomplished using a variety of methods also used in the PHABSIM software. We simulate depth for each donor cell (D_{don}) using a rating curve. Velocity (V_{don}) estimates are more complicated. When hydraulic data is available at a range of calibration flows, then a rating curve can be used to estimate velocity from flow. In two situations, the model opts to use Manning's equation with PHABSIM estimates of roughness coefficients at each calibration flow and slope estimates assigned on the basis of habitat type (Table 2-1). This occurs when the rating-curve estimates are unreasonable (i.e., $V_{don} < 0$ or $V_{don} > V_{cap}$) or when the number of wetted calibration flows for the cell is less than N_{minQ} . When streamflow exceeds an upper threshold Q_{max} , we determine that the PHABSIM estimates are no longer accurate and use a different hydraulic simulation method. The model still uses Manning's equation, but it assumes that all habitat types have converged to the same water surface slope of S_{ave} and that all roughness parameters have dropped to a specified value (N_{min}).

Fig. 2-1 Schematic of the procedure used to calculate depths, widths, and velocities for PHABSIM cells in receptor habitat units. Calculations are based on depths, widths, and velocities for cells in donor habitat units and on differences in the mean depth and width of the receptor and donor habitat units at a reference flow.

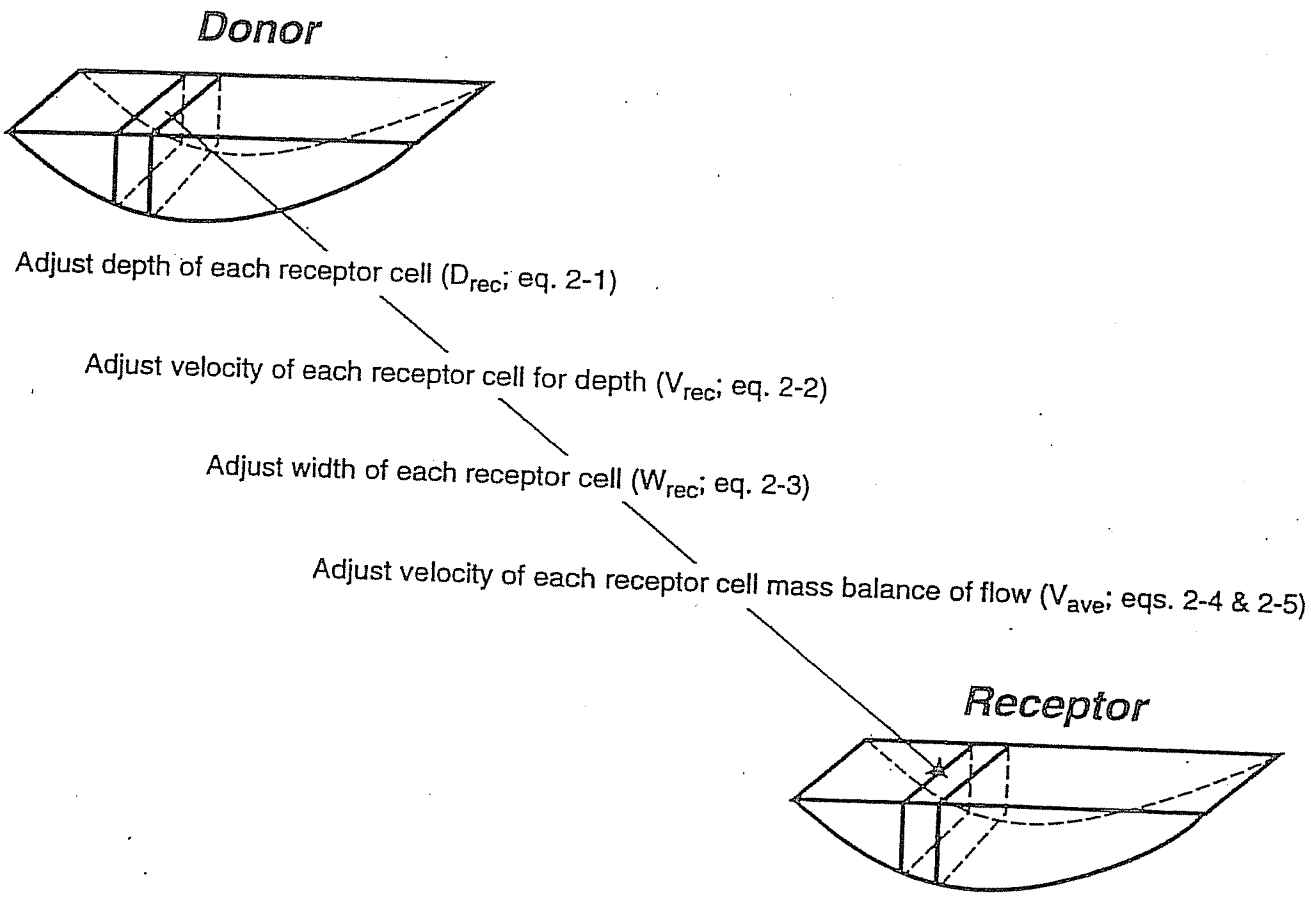


Table 2-1. Slope is selected at random for each habitat unit at the start of the simulation for use at unusually high flows. The following uniform distributions from which slope values are selected are adapted from Sullivan 1986, Table 5.3 and Fig. 5.2.

Mesohabitat type	Minimum slope (S_{min})	Maximum slope (S_{max})
Pool	0.0	0.01
Riffle	0.02	0.06
Pocket water	0.02	0.06
Run	0.01	0.02

To tailor hydraulic estimates for the PHABSIM transects to the receptor cells, we use known differences in the shape of the stream channel for the donor and receptor habitat units. The initial daily estimates of depth and velocity for receptor cells are adjusted based on differences between the donor and receptor habitat units at a reference flow. The adjusted daily depth for each cell in a receptor habitat unit (D_{rec}) is calculated as

$$D_{rec} = D_{don} + (D_{HU.don} - D_{HU.rec}) \ , \qquad \text{(eq. 2-1)}$$

where $D_{HU.don}$ and $D_{HU.rec}$ are the average depths at the reference flow for the donor and receptor habitat units, respectively. An adjusted depth of $D_{rec} \leq 0$ implies that the recipient cell is dry at the current flow.

The initial daily estimate of velocity assigned to a receptor cell from its corresponding donor cell (V_{don}) is corrected for the difference in depth between the donor and receptor cells at that day's flow. The equation is

$$V_{rec} = V_{don} \ (D_{don}/D_{rec})^{b_{vel}} \ , \qquad \text{(eq. 2-2)}$$

where the parameter b_{vel} is set to -0.5 (Milhous et al. 1989, Table II.2, page II.56, option 16 in IFG4).

We calculate the total width of wetted cells for each habitat unit for each day, and then adjust its width to ensure that the ratio of the width of a receptor habitat unit to the width of its donor habitat unit at the reference flow is maintained. The daily width for each cell in a receptor habitat unit (W_{rec}) is calculated as

$$W_{rec} = W_{don} \, (W_{HU,rec}/W_{HU,don}) \, , \qquad \text{(eq. 2-3)}$$

where $W_{HU,rec}$ and $W_{HU,don}$ are the mean widths at the reference flow for the receptor and donor habitat units, respectively.

The final step is to correct daily V_{rec} values to satisfy a mass balance constraint for flow. The estimated flow through each habitat unit (Q_{est}), based on the values for D_{rec}, W_{rec}, and V_{rec} for each cell, is

$$Q_{est} = \Sigma D_{rec} \, W_{rec} \, V_{rec} \, , \qquad \text{(eq. 2-4)}$$

where the summation is over all the cells in the habitat unit. Mass balance of flow is achieved by multiplying the V_{rec} value for each receptor cell by the velocity adjustment factor Q/Q_{rec} (Milhous et al. 1989, Table II.2), where Q is the measured streamflow. This adjusted value is the simulated average water column velocity (V_{ave}) for the receptor cell for that day, that is,

$$V_{ave} = (Q/Q_{est}) \, V_{rec} \, . \qquad \text{(eq. 2-5)}$$

This adjustment is made for all habitat units, including the donors.

2.2 Wetted Area of a Habitat Unit

The width of each receptor cell does not change with time, but the number of cells that are dewatered or dry may change with flow. The model keeps track of daily changes in the wetted width and wetted area of each habitat unit. This wetted area (A_{HU}) is used in representing availability of spawning habitat (Sect. 3) and feeding stations (Sect. 7).

2.3 Instream Cover

The type and amount of cover in a stream is typically of critical importance in influencing the daily bioenergetics and behavior of trout (see Sect. 7). Stream surveys often classify cover as instream cover (e.g., boulders, logs), undercut banks, overhead, and surface turbulence. The current version of the model considers only instream cover. Instream cover is important in providing shelter from high velocity while feeding (Sect. 5) or resting (Sect. 6), and from predators (Sect. 8). The fraction of the wetted area of a habitat unit with instream cover provided by boulders and woody debris (F_{cov}) is input for each habitat unit based on mesohabitat mapping at baseflow. Because we have no estimates for instream cover at other flows, we assume that instream cover is a constant fraction of A_{HU} at all flows.

SECTION 3 SPAWNING

This model provides a tool for evaluating the effects of flow and other factors on spawning success. Three examples of such effects are as follows. First, our model considers the timing of flow events in relation to spawning activity. The impact of extreme flows on the two trout species can be quite disparate because they spawn in different seasons. The pattern of high flows in winter months may have a role in preserving native rainbow trout populations in California streams by scouring the redds of the fall-spawning brown trout but not affecting the redds of rainbow trout, which spawn later in the spring.

Second, our model includes a formulation for the mortality of eggs and alevins because of construction of one redd on top of an existing redd (see Sect. 4.3.4, Superimposition). The amount and location of suitable spawning habitat will vary with flow, and data indicate that superimposition occurs more frequently when the density of spawners is high (T. Essington, University of Minnesota, St. Paul, MN).

Third, our model can be used to assess the indirect effects of flow on the ability of mature adults to survive in a stream and gain access to suitable spawning habitat. In the Tule River, the majority of spawners are Age 2; few individuals (especially rainbow trout) live to spawn twice. The low frequency of older spawners and repeat spawners likely involves velocity, depth, and prey availability, and thus, flow. For example, adults may require a certain amount of deep pool habitat; higher densities of large forage items may occur at higher, lower, or more stable flows; and risk of predation and energetic costs associated with spawning may be greater with some flow regimes than others.

In this section we describe our formulations for (1) sexual maturity, (2) timing and order of spawning, (3) dependence of spawning on flow and change in flow, (4) dependence of spawning on physiological condition, (5) selection of a habitat unit and cell, (6) multiple redds and spawning days, and (7) fecundity and adjustments to fecundity. Energetic costs are not considered in this representation of reproduction. Superimpostion is considered in Sect. 4 as one of the sources of mortality for eggs and alevins in a redd.

3.1 Sexual Maturity

Length and age of trout at sexual maturity can vary considerably between populations, between years, and between individuals of the same age. This variability is a function primarily of growth during the first 2 years of life. Sexual maturity for each trout in the model is specified on the first day of the spawning period (see Sect. 3.2 for definition of spawning period). Minimum age at sexual maturity is Age 1 for all species and both sexes. For each trout Age 1 and older, the probability of sexual maturity (P_{mat}) is represented as a linear function of length (L, mm) between the two points (L, P_{mat}) = (L_{mat}, 0.0) and (L_{spawn}, 1.0). Our values for the parameters L_{mat} and L_{spawn} are 170 mm and 250 mm for brown trout and 130 mm and 200 mm for rainbow trout (Moyle 1976). We use the same values for males and females. We do not have extensive site-specific data for the Tule River, California, but these length limits are consistent with incidental field observations (T. K. Studley, Pacific Gas & Electric Company, personal communication).

3.2 Timing and Order of Spawning

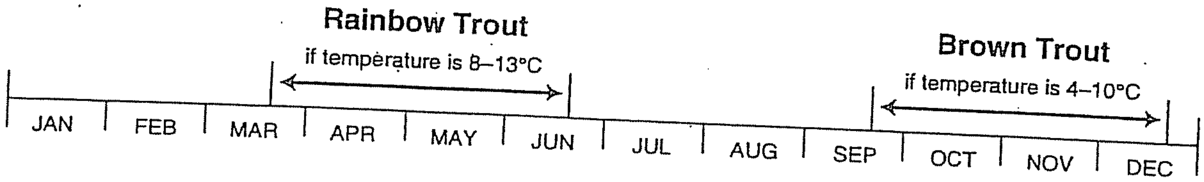
Lam (1988) emphasizes that photoperiod is the primary environmental cue for gonadal development, whereas temperature is the primary environmental cue for spawning. Sorensen (P. Sorensen, University of Minnesota, personal communication) envisions photoperiod as a controlling factor and temperature as a limiting factor (Fry 1971). Regardless of the terms, it is clear that both photoperiod and temperature influence the timing of spawning. It is also clear that brown trout and especially rainbow trout exhibit considerable phenotypic plasticity in the timing of spawning among populations.

In light of this information, we determine the timing of spawning as follows. We specify a spawning period by putting in start and end dates (J_{sp1}, J_{sp2}) for each species on a site-specific basis. Our dates for Segment 8 of the Tule River are October 1 (Day 274) and December 31 (Day 365) for brown trout and April 1 (Day 91) and June 30 (Day 181) for rainbow trout

(Fig. 3-1). Within these date periods, the temperature at which spawning occurs is assigned at random to each sexually mature female from a triangular distribution centered on the midpoint of the following species-specific temperature intervals (T_{spmin}, T_{spmax}): 4.0–10.0°C for brown trout and 8.0–13.0°C for rainbow trout (Billard 1992; Elliott 1984a; Moyle 1976; Wismer and Christie, 1987) (Fig. 3-1).

For many species, including brown and rainbow trout, temperature change in itself influences the timing of spawning. Hatchery operators commonly increase temperature over a period of hours and days to induce spawning and decrease temperature to delay spawning (Billard 1992). Peaks of spawning activity associated with rapid increases in temperature have also been observed in field data (e.g., Rose and Cowan 1993). In our simulations, we use actual average daily temperature regimes that typically include 2–3 day periods of increasing temperature and decreasing temperature both in the spring and the fall. Given this variability within a season, we use an algorithm similar to that developed by Rose and Cowan (1993) to simulate the day of spawning for each mature female as a function of water temperature (T). A female brown trout spawns in the fall on the first day (Day t) that T(t-1) is less than or equal to her assigned spawning temperature *and* $T(t-1) < T(t)$. A female rainbow trout spawns in the spring on the first day that T(t) is greater than or equal to her assigned spawning temperature *and* $T(t-1) < T(t)$. This algorithm is easily simplified when we use a sinusoidal temperature function rather than actual daily temperature data.

Fig. 3-1 Timing of spawning for brown and rainbow trout is determined in the model by specifying a temperature range within a calendar date window on a site-by-site basis. The dates and temperatures shown here are for Segment 8 of the Tule River, CA.



3.3 Dependence of Spawning on Flow and Change in Flow

Spawning activity of fish species inhabiting streams, especially species that construct redds (e.g., salmonids) and nests (e.g., centrarchids), can be delayed or disrupted by extremely high flows and by sudden changes in flow. Given this generality, spawning does not occur in the model if flow exceeds an upper bound, Q_{spmax}. The value selected for this parameter may be based on the flow where gravel starts to move, although it seems likely that extremely high flows that are not yet high enough to move gravel may be disruptive to spawning activity. In addition, conditions for redd construction and spawning are considered unacceptable when the relative change (i.e., increase or decrease) in flow from the previous day (ΔQ_{sp}) exceeds a threshold value (ΔQ_{spmax}). Our current best guess for this threshold is 20%, that is, a female does not spawn if

$$\Delta Q_{sp} = \mathrm{ABS}\{[Q(t) - Q(t-1)]/Q(t-1)\} \geq 0.2 \text{ ,} \qquad \text{(eq. 3-1)}$$

where ABS denotes absolute value.

3.4 Dependence of Spawning on Physiological Condition

A sexually mature female in the model spawns only if her condition factor (K) on the day she is scheduled to spawn exceeds a threshold, K_{sp}. Our estimate for this parameter for all three species is 0.6, which is somewhat greater than the minimum condition factor for survival (K_{min}) of 0.5. For a Pacific salmon species we would set $K_{sp} = K_{min}$. See Appendix 5 for a consideration of life history strategies and energetic tradeoffs between reproduction and survival.

3.5 Selection of a Habitat Unit and Cell

General characteristics of suitable redd sites for brown and rainbow trout are given in Beard and Carline (1991), Crisp and Carling (1989), Grost and Hubert (1990, 1991), and Witzel and MacCrimmon (1983). In addition, Studley et al. (1995, Appendix D) have developed site-specific, univariate suitability indices for velocity and depth for trout spawning habitat in the Tule River.

We have estimates at base flow for the fraction of bottom area judged suitable for spawning (F_{spawn}) for each habitat unit (Studley et al. 1995). These estimates are based on consideration of substrate (but not velocity and depth) for each pool, pocketwater, riffle, and run habitat unit at base flow.

In selecting a spawning site, we first select a habitat unit and then a cell within that habitat unit. Each habitat unit is assigned a probability of spawning (P_{spawn}), which is proportional to the percentage of spawning substrate estimated for that habitat unit (all F_{spawn} values are less than 0.1 in the segment of the Tule River we are simulating; Studley et al. 1995). Values of P_{spawn} are calculated as $P_{spawn} = f_{spawn} F_{spawn}$, where the value of the adjustment factor (f_{spawn}) is determined during model calibration to ensure that nearly all sexually mature trout do select a habitat unit for spawning; the value of f_{spawn} is the same for all habitat units. For each habitat unit evaluated by each trout, a value is selected at random from a uniform [0,1] distribution. If the value selected is less than or equal to the P_{spawn} value for that unit, the trout selects the unit. If the random value is greater than P_{spawn}, then the search for a habitat unit continues until one is found. Habitat units are evaluated one by one starting with the current unit, then moving upstream unit by unit to the first impassable cascade, and then back to the current unit and downstream unit by unit to the downstream end of the river segment. An alternative option for selecting a habitat unit is to have each trout spawn in its natal habitat unit, regardless of what unit it is in on the day of spawning. The concept of a natal habitat unit has meaning only in the context of multiyear simulations when progeny from the first spawning are themselves sexually mature and contribute to the new Age 0 year class.

Once a habitat unit is selected, a cell within that unit is assigned (see Sect. 7) so that we can simulate the water velocity and depth (as a function of flow) to which the redd is exposed from the day of spawning to the day of emergence of the last alevin from that redd. We require that the following two conditions for a cell be met on the day of spawning: (1) the depth (D) of the cell is greater than or equal to (d_{move} L), where d_{move} is the minimum water depth required both for spawning and for a PHABSIM cell to be habitable, defined as a fraction of the length (L) of the trout that is spawning; and (2) the average water column velocity (V_{ave}) of the cell is less than or equal to S_{max}, where S_{max} is the maximum swim speed (cm/sec) for the trout based on temperature and the trout's length (see Sect. 5). If no such cell is available in the habitat unit selected, the search for another habitat unit continues. No direct energetic cost is associated with a female selecting a habitat unit and cell for spawning.

In summary, selection of a habitat unit and cell for spawning in our model is a function of availability of suitable spawning substrate (F_{spawn} and f_{spawn}), water depth (D), and average water column velocity (V_{ave}). With additional research it should be possible to refine our formulation to consider other factors such as a tendency to select a suitable spawning site which already has a redd (T. Essington, University of Minnesota, St. Paul, MN).

3.6 Multiple Redds and Spawning Days

Both brown trout and rainbow trout females may build more than one redd and spawn on more than one day. However, we do not have information on mechanisms or frequency of occurrence. Consequently, each spawning female in the model constructs one redd and spawns on one day ($P_{onesp} = 1.0$). Although a male may spawn more than once and on different days, and eggs from a given female may be fertilized by sperm from more than one male (Scott and Crossman 1973), we do not represent these details in the model. We assume that mature males needed to fertilize eggs are never a limiting factor.

3.7 Fecundity and Adjustments to Fecundity

Fecundity (F, number of mature ova in the ovaries of a female on the day of spawning) is represented as a power function of length (L) on the day of spawning:

$$F = a_{fec} L^{b_{fec}} . \qquad \text{(eq. 3-2)*}$$

Considerable phenotypic variability exists among resident stream populations of both brown and rainbow trout (Avery 1985; Bromage et al. 1990; Elliott 1984a; McFadden and Cooper 1964). Our parameter values are $a_{fec} = 1.16$ and $b_{fec} = 2.54$, where L is total length in inches. These values are based on Avery's (1985) regression analysis for brown trout in eight Wisconsin streams, which we suspect result in fecundities that may be too high for trout in Sierra Nevada streams, such as the Tule River. We use the same values for brown and rainbow trout. We use fork length (FL) in millimeters in the model, which is changed to total length (TL) in inches to calculate fecundity using the relation TL = 1.03 FL/25.4 for brown trout and TL = 1.07 FL/25.4 for rainbow trout (Carlander 1969).

We multiply the fecundity (F) of each spawning female by $F_{eggs} = 0.9$ to get the number of fertilized eggs successfully deposited in a redd. Empirically, it is known that some fraction of mature ova in a female are lost because of resorption (Scott 1962), not being viable, being viable but not fertilized, or being viable and fertilized but not deposited in the redd (McFadden and Cooper 1964).

SECTION 4 DEVELOPMENT AND MORTALITY IN THE REDD

The growth and risks of mortality for the egg and alevin life stages differ sufficiently from those for subsequent stages that we describe our formulations for these nonfeeding and relatively well protected live stages separately in this section. We consider (1) the influence of female size on the size of alevins at emergence, (2) the influence of temperature on the daily development rate of eggs and alevins and the period of emergence from the redd, and (3) five risks of mortality while they are in the redd.

4.1 Influence of Female Size

Variability in size of eggs from a given female is minimal; a standard error of 1.0 mg dry wt or wet wt is typical (Bromage and Cumaranaturga 1988; Elliott 1984a). However, mean diameter and weight of eggs at spawning both increase with size of female (Avery 1985; Elliott 1984a). The percentage of eggs that hatch, percentage of alevins that emerge, and time to emergence do not appear to depend on either egg size or female size (Elliott 1984a). However, the size of newly hatched alevins and the size of alevins at emergence are positively correlated with egg size and female size (Elliott 1984a). The increased survival of fry which are larger at emergence was evident when newly emerged fry were kept in the laboratory without food. Elliott (1984a) found that survival time, measured in degree-days between emergence and death, increased linearly with increasing wet weight (mg) of the newly emerged fry. As an example, 50% of small, newly emerged alevins (140 mg wet wt) were dead after 125 degree-days without food, whereas 50% of large, newly emerged alevins (> 200 mg wet wt) were dead only after more than 225 degree-days. These results are in qualitative agreement with those of Bagenal (1969), who found survival significantly greater for brown trout fry from large eggs than those from small eggs.

The relevant finding from these experimental results for our trout model is that larger females produce larger eggs that result in larger alevins at the time of emergence. We summarize this finding with the following equation for length of fry at emergence (L_{fry}, mm) as a function of length of female parent ($L_{♀}$, mm):

$$L_{fry} = a_{fry} + b_{fry} L_{♀} . \qquad \text{(eq. 4-1)}$$

This straight line passes through the two points ($L_{♀}$, L_{fry}) = (170, 20) and (300, 30) for brown trout and (130, 20) and (220, 30) for rainbow trout. These points approximate the observed length range of sexually mature brown and rainbow trout in the Tule River and the observed length range of trout fry at emergence; they may require minor adjustment for other sites. Fry in the model that are larger at emergence may have a higher probability of survival, but this result is not directly coded into the model (see Sect. 8 on Mortality).

4.2 Period of Emergence

Development rate and number of days from fertilization to emergence must be well represented in this simulation model for several reasons. Brown and rainbow trout differ markedly in development rate. Rainbow trout have the fastest rate of embryonic development among salmonids at most temperatures (Billard 1992). This difference is accentuated when dealing with fall-spawning brown trout and spring-spawning rainbow trout. Brown trout eggs and alevins can be in a redd for 3–4 months, whereas rainbow trout eggs and alevins may be in a redd only 1–2 months. While in a redd the eggs and alevins are relatively protected from some sources of mortality, like predation, but they are less protected from other sources of mortality, like scouring and siltation associated with flood events.

The fertilized eggs and alevins in each redd are followed in the model as a cohort from the day of spawning to emergence as fry. Day of emergence is a function of the temperature regime between spawning and emergence (e.g., Anderson 1983). Because Embody's (1934) brown and rainbow trout data for the daily rate of development from fertilization to 50% emergence clearly indicate a curvilinear dependence on temperature, we selected a quadratic equation for the development rate (R_{dev}, 1/day) from fertilization to 50% emergence as a function of temperature. The fractional development (R_{dev}) that takes place on a given day is calculated as the reciprocal of the number of days from fertilization to 50% emergence if the temperature were held constant at the temperature occurring on that day (Rose and Cowan 1993). Our equation is

$$R_{dev} = a_{dev} + b_{dev}\,T + c_{dev}\,T^2 \,. \qquad \text{(eq. 4-2)*}$$

Day of 50% emergence is determined by accumulating daily values for R_{dev} until the day the cumulative sum ($RSUM_{dev}$) equals or exceeds 1.0.

We estimated parameter values for eq. 4-2 separately for the two species using regression analysis and data from Embody (1934) on number of days required for 50% of a batch of fertilized eggs to hatch into alevins at various constant temperatures. The more limited data on number of days to 50% hatch from Leitritz and Lewis (1980) are in excellent agreement for both species. Elliott's (1984a) laboratory and field data and hyperbolic regression model for brown trout in England are also in good agreement except at the lowest and highest temperatures. We use the results from Elliott's (1984a) analysis for brown trout to extrapolate Embody's (1934) data for both brown and rainbow trout to number of days required for 50% of a batch of fertilized eggs to become free-swimming fry.

Emergence of alevins from individual redds in Elliott's (1984a) laboratory experiments occurred over a period of 7–15 days. Differences in day of emergence may be due to intrinsic differences between eggs and between alevins and extrinsic differences in the microhabitat within the redd. More importantly, these differences can have significant consequences for the population in a stream when flow and temperature vary from day to day. We approximate this variability in day of emergence from each redd with a uniform distribution (a triangular distribution would be a logical alternative) centered on the expected day for 50% emergence. Emergence from a given redd starts on the day that $RSUM_{dev}$ for that redd = $RSUM1_{dev}$, where $RSUM1_{dev}$ is a specified value for $RSUM_{dev}$ with a value slightly less than 1.0. The expected day for 50% emergence is estimated by extrapolating the rate of increase in $RSUM_{dev}$ on the day $RSUM_{dev}$ reaches $RSUM1_{dev}$ to a value of 1.0. This calculation is made once for each redd. The uniform distribution is then centered on the day $RSUM_{dev}$ is expected to reach 1.0, with a spread of plus and minus the expected number of days for $RSUM_{dev}$ to increase from $RSUM1_{dev}$ to 1.0. Our value for $RSUM1_{dev}$ is 0.95, which was determined during model calibration to result in an average period of emergence of 2–3 weeks; we use the same value for both species.

4.3 Risks of Mortality

Although eggs and alevins in a redd are relatively well protected, several risks of mortality still exist. In our model, we represent the risk of mortality due to (1) dewatering, (2) scouring,
(3) temperature, (4) superimposition, and (5) background.

4.3.1 Dewatering

Before emergence from the redd, dewatering and reduction in water levels can result in mortality of eggs and alevins from desiccation, reduced levels of dissolved oxygen, and exposure to low or high air temperatures. Because of the protection provided by being buried in a redd, these stresses associated with dewatering probably occur over a period of several days (S. Williamson, National Biological Survey, Fort Collins, CO, personal communication). We assume that a redd is dewatered if the water depth in the cell in which the redd is located is zero. We set the daily probability of mortality due to dewatering (P_{dewat}) at 0.5 for the cohort of eggs and alevins in a given redd each day that redd is dewatered. Empirical data are needed to support this estimate, beyond the observation that not all eggs and alevins in a redd are dead after 24 h of being dewatered.

4.3.2 Scouring

High flows can cause mortality of eggs and alevins because of scouring and physical disruption of the redd, resulting in eggs and alevins being washed downstream or buried in silt. Anderson (1983) and Elliott (1976a) for brown trout and Seegrist & Gard (1972) for rainbow and brook trout report loss of eggs and alevins during spates and floods. Water velocity increases with flow in almost all habitat types (Sullivan 1986), and Elliott (1976a) found that both the number and density of brown trout eggs in drift samples from two streams in different years increased with increasing water velocity.

We represent the daily risk of loss of a redd from scouring (P_{scour}) as an increasing logistic function of average water column velocity (V_{ave}, cm/sec):

$$P_{scour} = \exp(V_{ave})/[1.0 + \exp(V_{ave})] \;. \qquad \text{(eq. 4-3)*}$$

We control the position of this logistic curve along the velocity axis and the steepness of its slope by specifying two points through which the function passes. We selected the coordinates for these two points in the following manner. The very low abundance of the 1991 year class of brown trout in the Tule River has been attributed to the exceptionally high flows on March 4, 1991. Presumably, these flows resulted in velocities high enough to scour most of the brown trout redds constructed during the preceding fall. In our simulation model for Segment 8 of the Tule River, we varied the velocity coordinates for these two points until we achieved our target of scouring 75–80% of the brown trout redds. The coordinates (V_{ave}, P_{scour}) for these two points are (1.0 m/s, 0.05) and (1.3 m/s, 0.95) for redds of all species. We recommend for other sites that the coordinates for these two points be based on site-specific data.

We have considered more mechanistic formulations for scouring based on hydraulic principles (e.g., tractive-force calculations; G. M. Kondolf, University of California, Berkeley, CA, personal communication). However, we do not see a way to do this without greatly increasing the complexity of how we relate flow to hydraulics on a finer spatial scale. One approach for specifying the flow required to flush gravels, and thus scour redds, did not work well in high-gradient, boulder-bed streams where gravels suitable for spawning commonly occurred in pockets behind boulders (Kondolf et al. 1987).

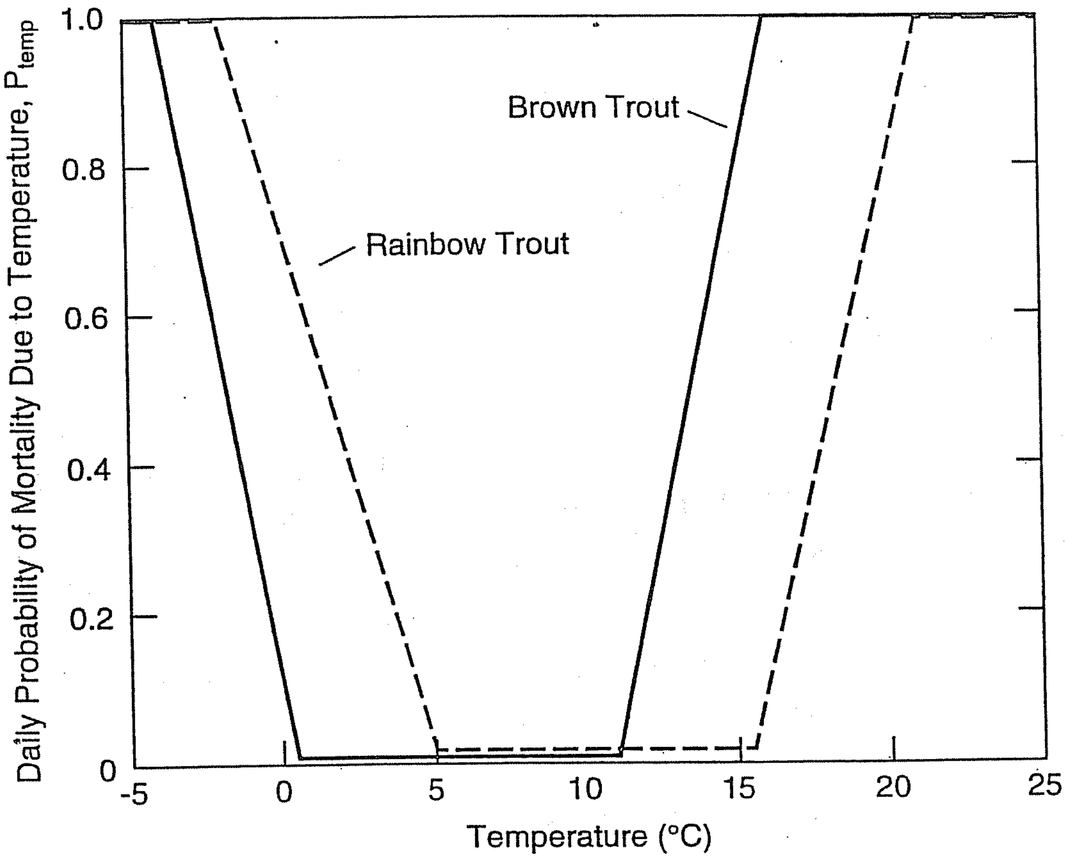
4.3.3 *Temperature*

Mortality of eggs and alevins in a redd due to temperature alone appears to be limited to temperature extremes (Embody 1934; Murray and McPhail 1988). We represent this generality in our model by defining a daily probability of mortality due to temperature (P_{temp}) that is 0.0 within an optimal temperate range (T_2 to T_3) and that increases linearly to 1.0 as temperature decreases to T_1 and increases to T_4. Our formulation is as follows (Fig. 4-1):

$$\begin{aligned} P_{temp} &= 1.0\,, && \text{if } T < T_1\,,\ \text{or } T > T_4\,, \\ &= 0.0\,, && \text{if } T_2 \le T \le T_3\,, \\ &= (T_2 - T)/(T_2 - T_1)\,, && \text{if } T_1 \le T \le T_2\,, \text{ and} \\ &= (T - T_3)/(T_4 - T_3)\,, && \text{if } T_3 \le T \le T_4\,. \end{aligned} \qquad \text{(eq. 4-4)}$$

These four temperature thresholds are -4.0, 0.5, 11.0, and 16.0°C for brown trout and -1.0, 5.0, 15.0, and 21.0°C for rainbow trout (Wismer and Christie 1987) (Fig. 4-1). Data indicate that development of alevins is somewhat more sensitive to temperature extremes than development of eggs (Murray and McPhail 1988 for the five Pacific salmon species; Timoshina 1972 for rainbow trout). We are not aware of comparable data for brown trout and have not incorporated this difference in temperature sensitivity in our formulation.

Fig. 4-1 Daily probability of mortality for eggs and alevins as a function of temperature for brown and rainbow trout.



4.3.4 Superimposition

Superimposition is the construction of one redd on top of an existing redd, unavoidably resulting in the mortality of some fraction of the eggs and alevins in the original redd. Such losses can be substantial for stream populations of brown and rainbow trout (T. Essington, University of Minnesota, St. Paul, MN, personal communication).

The extent of superimposition is likely to be site specific, depending on the amount and patchiness of suitable spawning habitat and the density of spawners. In Segment 8 of the Tule River, spawning habitat is distributed in numerous small pockets in eddies associated with boulders in pocket water and pool habitat units. This distribution of suitable spawning habitat may reduce the frequency of superimposition, compared to a distribution characterized by a limited number of larger sites with suitable spawning habitat. Another factor known to be important to trout in selection of a spawning site is areas of groundwater upwelling (Curry et al. 1994; Ottoway et al. 1981); however, this is not a factor in the segment of the Tule River we are modeling. Finally, there is growing evidence to indicate that a trout may preferentially select a suitable spawning site where another trout has already constructed a redd instead of another suitable spawning site without an existing redd (T. Essington, University of Minnesota, St. Paul, MN, personal communication). We are not aware of any quantitative data on superimposition for Sierra Nevada trout populations.

In the absence of quantitative data but with the above generalities in mind, we formulated a geometric model of superimposition for low gradient streams and rivers with a continuous area of suitable gravels, and a second model for high gradient streams with spawning gravels that occur in pockets behind boulders. The second approach seems more appropriate for the Tule River and is as follows.

In high gradient streams, we estimate the maximum number of nonoverlapping sites for redds in a habitat unit as

$$N_{sites} = f_{spawn}\ F_{spawn}\ A_{HU}/A_{redd}\ . \qquad \text{(eq. 4-5)}$$

The variable A_{HU} is the wetted area (m^2) of the habitat unit (which is a function of flow; see Sect. 2), and A_{redd} is the average area for a redd, for which we use a value of 0.3 m^2 for all model trout that spawn (Ottoway et al. 1981). F_{spawn} is the fraction of bottom area in a habitat unit judged suitable for spawning. Estimates of this fraction, considering substrate only, are available for each habitat unit in the Tule River based on a mesohabitat survey done at baseflow (Studley et al. 1995, Table 4.2-1); we assume that the F_{spawn} value for a habitat unit applies at all flows. The parameter f_{spawn} is an adjustment factor for the fraction of the area of a habitat unit suitable for spawning; the value for this parameter is determined during model calibration to ensure that most trout spawn in a suitable cell and to control the number of times superimposition occurs.

Each spawning female is randomly assigned a site from the set of possible sites (N_{sites}). If one or more redds exist at this site, then superimposition occurs and a fraction (F_{lost}) of the eggs and alevins in each of the existing redds is lost. Reasonable values for F_{lost} are probably in the range 0.5–1.0, and may vary depending on site-specific characteristics and availability of spawning habitat.

4.3.5 Background

The parameter P_{bkgd} represents the daily probability of mortality of eggs and alevins from unspecified causes. In the absence of superimposition and extremes in flow and temperature, some of the eggs and alevins in a redd die each day. A cumulative probability of mortality of 0.1 during the entire period of incubation due to these background risks seems reasonable (Avery 1980; Elliott 1984a; McFadden and Cooper 1964). As an example, $P_{bkgd} = 0.000878$ for brown trout and 0.00175 for rainbow trout correspond to the same probability of mortality (i.e., 0.10) during the period of incubation, assuming 120 days (e.g., December–March) of incubation for brown trout and 60 days for rainbow trout (e.g., April–May or May–June). The species-specific values for P_{bkgd} are adjusted during model calibration to influence the number of fry that emerge and to fit the number of juveniles observed in the fall.

SECTION 5 GROWTH: FORAGING AND CONSUMPTION

Our trout model is designed to link flow, microhabitat, and trout behavior to the daily growth of each trout. The bioenergetics model describing the daily growth of individual trout is

$$W(t+1) = W(t) + (1/a_{cal})\,(C - E_{eg} - E_{ex} - E_{SDA} - R), \qquad \text{(eq. 5-1)}$$

where W(t) is the wet weight (g) of the trout on day t, C is energy consumed (cal/day), and the energy losses (all in cal/day) are: E_{eg} (egestion), E_{ex} (excretion), E_{SDA} (specific dynamic action), and R (respiration). The constant a_{cal} converts calories of trout to grams wet weight of trout and has a value of 1000 cal/g for Age 0 trout and 1400 cal/g for Age 1 and older trout (Hewett and Johnson 1992). The most critical links between flow, habitat, and trout energetics in streams relate to foraging and consumption (i.e., the variable C in eq. 5-1). Our representation of foraging and consumption are described in this section. Our representation of energetic costs and changes in length and physiological condition are described in Sect. 6.

While some fish ecologists suggest that activity respiration costs dominate the energetics of stream fishes (Rincon and Lobon-Cervia 1993; Boisclair and Leggett 1989), most identify consumption as the most uncertain and variable term in eq. 5-1 (Hill and Grossman 1993; Hughes and Dill 1990; Puckett and Dill 1985). Current understanding about trout foraging permits us to make several generalizations. Trout are visual foragers that feed primarily on drifting invertebrate prey in streams (Bachman 1984). This being said, most studies on foraging comment on the opportunistic nature of trout feeding. There is general agreement that larger prey items (> 2 mm) are preferentially included in the trout diet (Bannon and Ringler 1986; Hill and Grossman 1993; Bisson 1978; Skinner 1985). Large trout, particularly brown trout, may feed on small fish, including trout (Bachman 1984). Behavioral aspects of trout feeding have been the subject of a great deal of research. Most studies have found that drift feeding (and agonistic behavior) is more common for trout holding a feeding station, while benthic feeding is more common (and agonistic behavior is less common) for individuals in pools not associated with a feeding station (Tanida et al. 1989; Grant and Noakes 1987, 1988; Puckett and Dill 1985). Higher consumption rates (biomass of prey consumed per time) for trout holding a feeding station as compared to those not holding a station have been observed in some, but not all, behavioral studies (Grant and Noakes 1987, 1988).

Our model of trout foraging is relatively simple. Because studies generally do not indicate prey depletion by drift foragers (or benthic foragers), we treat space (i.e., feeding stations and instream cover), rather than prey, as the contested resource. This approach allows us to avoid simulating the dynamics of each individual prey population. Experience with other models of foraging by stream fishes has shown that attempting to simulate prey dynamics contributes more uncertainty than predictive power (Hill and Grossman 1993; Jager et al. 1993). Because fish prey are so seldom found in the stomachs of Tule River trout (see Sect. 8), the current version of our model simulates feeding on invertebrate prey, but not on fish. The *spatially-explicit nature* of this model allows us to follow the lead of others (e.g., Fausch 1984; Hill and Grossman 1993; Hughes and Dill 1990), who successfully predicted habitat use and growth with simple models relating drift rate, capture efficiency, and energetic costs to velocity. Finally, the *individual-based nature* of this model enables us to explore the consequences of different behavioral tactics adopted by individual trout.

In this section, we discuss (1) behavioral tactics associated with drift and benthic foraging, (2) consumption rate, including consideration of reactive distance and formulations for drift and benthic consumption, (3) foraging velocity while drift and benthic feeding, (4) daily consumption, including consideration of time-limited and digestion-limited consumption, (5) maximum daily consumption as a function of the weight of the trout and temperature, and (6) a nonforaging option used in calibrating and debugging the model.

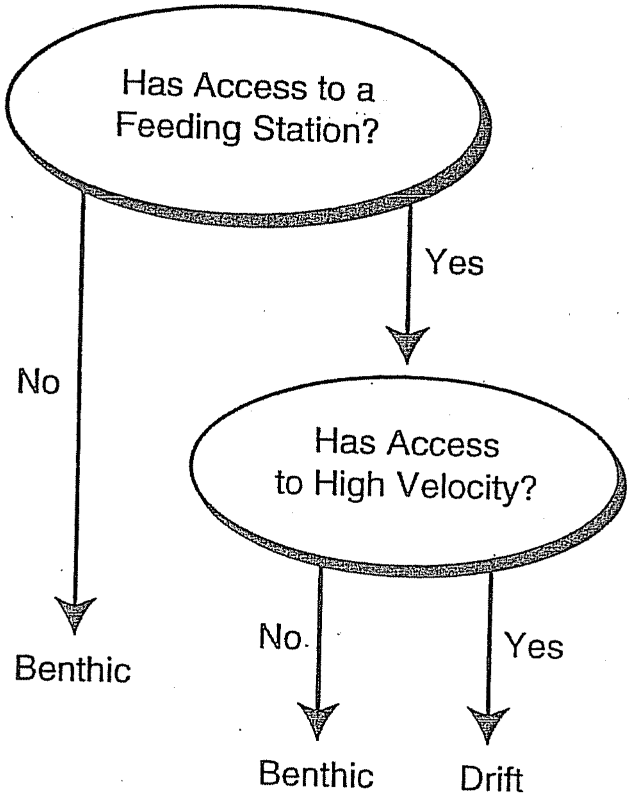
5.1 Behavioral Tactics

In modeling foraging, we provide the capability to evaluate the energetic tradeoffs between alternative behavioral tactics. To do this, we adopt several simplifications of reality that reflect current understanding about trout with access to a feeding station ("stayers") and those without ("movers"). Our model operates on a daily time step, so we assume that a trout's choice of tactic applies for an entire day. Clearly, this is not the case in the field. Grant and

Noakes (1987) observed that "individuals often switched from moving to staying many times during a 15-min observation," and others have observed benthic feeding by individuals holding a feeding station. Such switching more likely occurs for trout in slow-moving water (e.g., pools) than for trout in riffles. Over a period of days, the model trout have opportunities to change tactics, and thus, the penalty imposed by the choice of a daily time step should be minor.

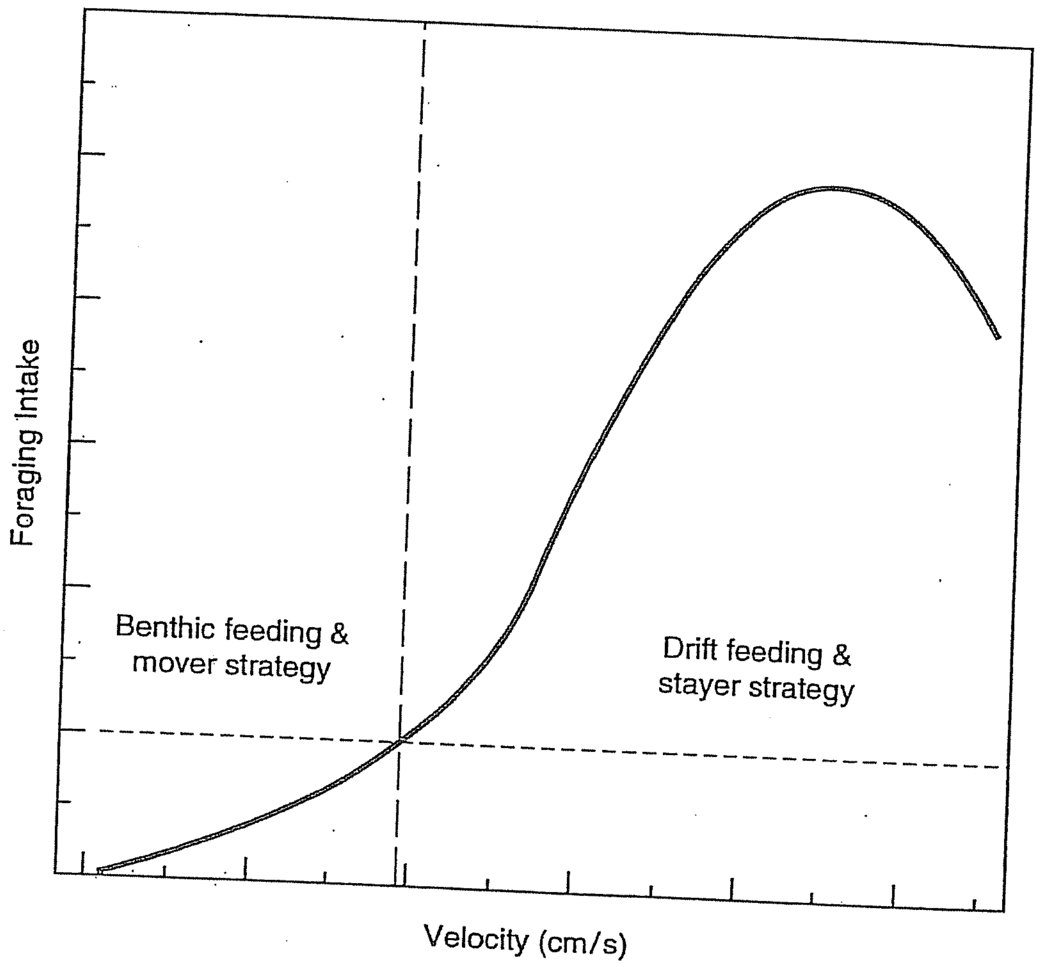
Each trout is characterized each day as having a feeding station ("stayer") or not ("mover") (Fig. 5-1) and forages either in the water column on drifting prey or near the stream bottom on benthic prey. We require trout without a feeding station to feed on the benthos. For trout with a feeding station, we calculate a rate of prey consumption for both drift and benthic foraging and allow the trout to feed in the mode that provides the higher consumption rate, as described in the following subsections.

Fig. 5-1 Paradigm for foraging tactics for trout. Each model trout on each day has a feeding station (stayer) or not (mover) and forages either in the water column on drifting prey or near the stream bottom on benthic prey. We require a trout without a feeding station to feed on benthos. For a trout with a feeding station, we calculate a rate of prey consumption for both drift and benthic foraging and allow the trout to feed in the mode that provides the higher consumption rate.



According to this foraging paradigm, feeding on drift is most profitable at intermediate velocities (Fig. 5-2). The rate of drift intake (biomass of drift prey consumed per time) falls below that of benthic intake at low velocities because the rate of delivery of drift (number or biomass of prey items available per time) from upstream decreases. The rate of drift intake also falls below that of benthic intake at high velocities, in this case because the velocity is so high the trout cannot effectively hold position at a feeding station and forage. This pattern has been observed in several stream fishes, with maximum drift consumption rates at a velocity (at the point of prey capture) of 7.5 cm/s for brook charr (Grant and Noakes 1987) and 12 cm/s for smallmouth bass (Simonson and Swenson 1990). At a given velocity, the maximum drift consumption rate in our model increases both with temperature and the length of the trout. Ideally, the velocity selected by a drift-feeding trout is the velocity that maximizes its consumption for that day, that is, an optimal feeding velocity. However, the trout may have to settle for a lower feeding velocity if the optimal feeding velocity is greater than what is available in the water column or if the optimal feeding velocity exceeds the fish's maximum swim speed (see Sect. 5.3.1).

Fig. 5-2 A conceptual graph of foraging intake as a function of velocity for model trout that feed on the benthos and have no drift-feeding station ("movers") and for model trout that feed on drift ("stayers"). Simulating consumption rate (g wet wt of prey consumed per time) involves each trout selecting benthic or drift feeding for a given day. The choice depends on which mode of feeding provides the higher consumption rate. See text for further discussion.



5.2 Consumption Rate

Consumption rate (W_{prey}, grams wet weight of prey consumed per time), which in part determines daily consumption, is discussed in this subsection. The velocity at which the trout forages (V_f) influences consumption rate and is discussed in Sect. 5.3. The reactive distance of a trout and the supply of prey are the two variables we use to predict consumption rate. In the first subsection below, we describe our equation for reactive distance. Following that, the consumption rate models for drift-feeding and benthic-feeding trout are described.

5.2.1 Reactive Distance

Reactive distance is the distance between a trout and a prey item at which the trout reacts to having seen the prey item by initiating a strike. Reactive distance for drift foragers decreases as water velocity (V, cm/s) increases (Godin and Rangeley 1989; Grant and Noakes 1987; Hill and Grossman 1993; Hughes and Dill 1990) and increases with temperature (T, °C) and length (L, mm) of the trout. We used empirical data from experiments by Hill and Grossman (1993) and logistic regression to develop a model for the probability of capture (P_{cap}) as a function of these three variables and the distance between the prey and the trout (PD, cm). We use the ratio of water velocity to trout length as a variable that reflects the relative water velocity in body lengths per second. Our equation is

$$P_{cap} = \exp(Y)/[1.0 + \exp(Y)] \text{ , where} \qquad \text{(eq. 5-2)*}$$

$$Y = a_{RD} + b_{RD}\ V/L + c_{RD}\ T + d_{RD}\ PD \text{ .}$$

To convert this expression into a model for reactive distance (RD, cm), we define RD as the distance between trout and prey that results in a 90% probability of capture ($P_{cap} = 0.9$) and solve eq. 5-2 for RD (in place of PD):

$$\begin{aligned} RD &= L\ \{-\ln[0.9/(1-0.9)] + a_{RD} - b_{RD}\ V/L + c_{RD}\ T\}/d_{RD}\ , && 0 < RD \le RD_{max}\ , \quad \text{(eq. 5-3)*} \\ &= 0\ , && RD \le 0\ , \\ &= RD_{max}\ , && RD > RD_{max}\ , \end{aligned}$$

where RD_{max} is the maximum reactive distance defined in body lengths and converted to centimeters.

We use this equation for both drift and benthic feeding. Other abiotic factors (e.g., light levels, turbidity; Vinyard and O'Brien 1976, Barrett et al. 1992) and biotic factors (e.g., characteristics of the prey) that influence reactive distance in a stream have not been included in the model.

5.2.2 *Drift Consumption Rate*

The consumption rate on drift prey (W_{prey}, grams wet weight of prey in the drift consumed per time) is a product of a prey supply rate and the foraging velocity of the trout. The supply rate of drifting prey has been found to increase with velocity (Fausch 1984; Grant and Noakes 1987; Statzner et al. 1985). We simulate this supply rate using a linear model by Fausch (1984). We select a value for m_{drift} as part of calibrating the model, for which we require reasonable agreement between simulated values and field data on stomach fullness (see Sect. 9). Each day for each trout we calculate an average rate of consumption of drifting prey as

$$W_{prey} = \pi\, RD^2\, m_{drift}\, V_f\,, \qquad \text{(eq. 5-4)}$$

where $\pi\, RD^2$ is the cross-sectional area of a cylinder with radius RD (cm), and V_f (cm/s) is the foraging velocity of the trout while drift feeding (see Sect. 5.3.1).

5.2.3 *Benthic Consumption Rate*

The consumption rate of benthic prey (W_{prey}) also is a product of prey supply and the foraging velocity of the trout:

$$W_{prey} = 2RD\, f_B\, N_B\, V_f\,. \qquad \text{(eq. 5-5)}$$

The width of a strip of stream bottom searched by a trout as it moves around is calculated as twice the reactive distance (2RD); details such as truncated visual fields are not considered. The density of benthic prey biomass (N_B) in Segment 8 of the Tule River averaged over all four seasons between 1986 and 1991 was 0.0013 g wet wt/cm^2 (Studley et al. 1995, Table 4.4). We also select a value for the fraction of benthic prey available to trout (f_B) as part of calibrating the model, for which we require reasonable agreement between simulated values and field data on stomach fullness (see Sect. 9). The foraging velocity (V_f) while benthic feeding is described in Sect. 5.3.2.

5.3 Foraging Velocity

To use this foraging model, we must identify a velocity (V_f) used by the trout while foraging. This can be thought of as an average of the velocities experienced during feeding activity and represents a key link between flow, habitat, and trout energetics. For drift feeders, V_f can be thought of as somewhere between a nose or focal velocity (measured at the holding position of the trout) and a strike velocity (measured at the point of contact with the prey). For benthic feeders, a water velocity near the stream bottom is more appropriate.

5.3.1 Drift-Foraging Velocity

For drift-feeding trout, foraging velocity (V_f) is the minimum of V_{opt}, V_{max}, and S_{max}, which are as follows. The optimum drift-foraging velocity (V_{opt}) is defined as that velocity that maximizes the drift consumption rate (see eq. 5-4). The optimum is found by taking the partial derivative of W_{prey} with respect to V_f, substituting eq. 5-3 for reactive distance (RD), setting this partial derivative equal to zero, and solving for V_f, which we denote as V_{opt}:

$$V_{opt} = \{a_{RD} - \ln[0.9/(1.0 - 0.9)] + c_{RD}\ T\}\ L/3b_{RD}\ . \qquad \text{(eq. 5-6)}$$

If possible, a trout forages at V_{opt}. However, first we have to determine whether this optimum is available to a trout in its current PHABSIM cell. To be available, V_{opt} must be less than the maximum velocity in the water column (V_{max}) and also less than the fish's maximum swim speed (S_{max}).

We estimate V_{max} from the average water column velocity in the PHABSIM cell using one of two methods. The first method assumes a logarithmic velocity profile, and we estimate surface velocity based on the water surface slope (S), where slope depends on mesohabitat type (but not flow). Sullivan (1986) provides a nice paradigm for mesohabitat classification with the first level of classification based on water surface slope: pools (S = 0.00 to 0.01); runs (S = 0.01 to 0.02); and riffles and pocket waters (S = 0.02 to 0.06). For the first method, maximum (surface) velocity (V_{max}) depends on average water column velocity (V_{ave}), depth (D), water surface slope (S), and a constant related to water density (k_0 = 0.4) (Gray and Wigham 1973):

$$V_{max} = V_{ave} + (9.81\ D\ S)^{0.5}/0.4\ . \qquad \text{(eq. 5-7)}$$

Alternatively, V_{max} can be estimated by using an empirical regression equation with a_{Vmax} = 56.3 cm/s and b_{Vmax} = 1.59 (Sullivan 1986):

$$V_{max} = a_{Vmax} + b_{Vmax} V_{ave} . \qquad \text{(eq. 5-8)}$$

Note that this second method does not account for differences between mesohabitat types or flow.

For both methods, we increase V_{max} for all PHABSIM cells in pools by a constant amount (V_{add}) because trout foraging on drift in pools tend to locate in the fast water coming into the pool from upstream. Our current value for V_{add} is 5 cm/s.

Finally, we require that the foraging velocity (V_f) does not exceed a trout's maximum swim speed, S_{max}:

$$S_{max} = a_{swim} W^{b_{swim}} \exp(c_{swim} T) . \qquad \text{(eq. 5-9)*}$$

Maximum swim speed is defined as the maximum swim speed a fish can sustain for a specified time (typically 1 h; Brett and Glass 1973). Values for the three parameters are based on Stewart (1980).

In summary, drift-foraging velocity (V_f) is the minimum of V_{opt}, V_{max}, and S_{max}.

5.3.2 Benthic-Foraging Velocity

For benthic-feeding trout, foraging velocity (V_f) is equal to the maximum of the velocity near the stream bottom (V_{bot}) and a trout's optimal swim speed (S_{opt}). Sullivan (1986) compared velocities at 4.0 cm above the bottom as a fraction (f_{bot}) of the average water column velocity (V_{ave}) for a number of mesohabitat types and velocity profiles for fourth order streams in the Cascade mountains of Washington. She found the product f_{bot} V_{ave}, with f_{bot} = 0.67, to be a good estimate of V_{bot} for all mesohabitat types. A trout's optimal swim speed (S_{opt}) is calculated as

$$S_{opt} = d_{swim} W^{e_{swim}} \exp(f_{swim} T) . \qquad \text{(eq. 5-10)*}$$

Optimal swim speed is defined as that swim speed which maximizes growth rate (Ware 1975). The three parameters in S_{opt} were estimated for trout weighing ≤ 150 g wet wt based on Rand et al. (1993), and for trout weighing > 150 g wet wt based on Stewart et al. (1983).

5.4 Daily Consumption

To simulate the consumption of individual trout on a daily basis, we multiply each trout's consumption rate as determined above by the time spent foraging (t_{activ}), where the daily consumption (W_{eat}, g wet wt of prey per day) is constrained either (a) by the time available for visual feeding or (b) by the maximum quantity of prey that the trout can digest in a day (C_{max}):

$$\begin{aligned} W_{eat} &= t_{activ}\, W_{prey}\,, & W_{eat} &< C_{max}\,, \\ &= C_{max}\,, & W_{eat} &\geq C_{max}\,. \end{aligned} \qquad \text{(eq. 5-11)}$$

Simulating the time spent foraging allows us to partition the day to reflect higher energetic costs and predation risks during periods of feeding activity.

5.4.1 Time-Limited Daily Intake

A trout that is time-limited in its consumption can also be thought of as limited by the availability of prey. The maximum number of hours during which a trout can feed (t_{actmx}) changes daily over the year with time of sunrise and sunset based on latitude (Brock 1981). Because trout feed to some extent at night, especially during the hour before sunrise and after sunset, we have modified Brock's (1981) formulation to include two additional hours of activity every day. A number of recent articles highlight that both brown and rainbow trout of all ages are active primarily at night (rather than day) during the winter and that some foraging occurs at night when there is adequate starlight or moonlight (e.g., Smith and Griffith 1994). Because we use a daily time step, it does not matter whether trout are active during day or night. What does matter is that t_{actmx} approximates the maximum number of hours trout are active on a daily basis and that changes in foraging success between daylight and nocturnal activity are adequately represented. Note that by using a reactive distance that assumes daylight conditions (eq. 5-3), foraging success may be overestimated during winter.

In calibrating the model, we found it useful to introduce a weight-dependent demand function that reduces the maximum number of hours a trout is active (t_{actmx}) at a decreasing rate as trout weight increases. The equation is

$$\text{Adjusted } t_{actmx} = (\text{Unadjusted } t_{actmx}) \,/\, W^{f_{dem}} , \qquad \text{(eq. 5-12)}$$

where the value of the parameter f_{dem} is determined during model calibration. Including this adjustment allowed us to do a better job of simulating observed lengths of Age 2 and Age 3 trout, while still simulating observed lengths of Age 1 trout.

5.4.2 Digestion-Limited Daily Intake

The variable t_{activ} in eq. 5-11 is the time spent foraging by a trout. If t_{activ} is less than t_{actmx}, it implies that the trout was satiated before being visually limited by low light levels. In practice, rations are small enough that t_{activ} generally equals t_{actmx} and realized consumption is less than maximum consumption (see Sect. 5.5 on C_{max}). Exceptions can occur when the digestion rate is low at extreme temperatures. Exceptions could also occur during periods of high prey abundance (e.g., mayfly hatches), which we have not included in the model.

5.4.3 Conversion from Wet Weight to Calories

Once the wet weight of prey consumed on a given day has been simulated for an individual trout (W_{eat}), this biomass is converted to units of calories of prey consumed on that day (i.e., the term C in eq. 5-1). The caloric value of prey consumed per day is calculated by separating prey consumed into fish and invertebrates, because these two prey types commonly differ substantially in energy density. Our conversion factors are 1000 cal/g wet wt of fish prey and 600 cal/g wet wt for invertebrate prey (Hewett and Johnson 1992; Rand et al. 1993; Roell and Orth 1993). Thus, the caloric value of what is consumed each day by a trout is

$$C = [1000\, F_{fish} + 600\, (1-F_{fish})]\, W_{eat} , \qquad \text{(eq. 5-13)}$$

where F_{fish} is the proportion of fish in the prey consumed. For Segment 8 of the Tule River, essentially all prey consumed are invertebrates (see Sect. 8; also Studley et al. 1995).

5.5 Maximum Consumption

When prey abundance exceeds the rate at which trout can digest food, daily consumption is limited by an upper physiological bound. In stream systems, this is most likely to occur when digestion is slowed by extreme temperatures or other stresses or when food is unusually abundant (e.g., a mayfly emergence). In the model, we represent maximum consumption (C_{max}, g wet wt of prey consumed per day) as a function of the weight of the trout (W, g wet wt) and temperature (T, °C) (Hewett and Johnson 1992):

$$C_{max} = a_{Cmax} \, W^{b_{Cmax}} \, f(T) \; . \qquad \text{(eq. 5-14)*}$$

The value for a_{Cmax} is estimated in calibrating the model. Our calibration criterion involving this parameter is that maximum weight-specific consumption (i.e., g wet wt of prey consumed per g wet wt of trout per day) at optimum temperatures is in the range of 10–20% for Age 0 trout and 5–15% for Age 1 and older trout. Our estimate for b_{Cmax} is 0.76 for all three species (Rand et al. 1993; Stewart 1980).

We used a temperature model developed by Thornton and Lessem (1978) to represent the function f(T) in eq. 5-11; see Appendix 4 for details. The parameter values for brown trout are based on our nonlinear, least-squares fit to the results of Elliott's extensive laboratory experiments using hatchery brown trout in which he measured maximum consumption over a range of temperatures and sizes of trout (Elliott 1975a, 1975b, 1975c, 1976b). Elliott notes that it would have been preferable to use wild trout instead of hatchery trout, but wild trout usually refused to feed in the experimental tanks. Most hatchery trout readily took food at temperatures between 6 and 19°C, but were inactive and reluctant to feed at temperatures below 6°C, and were very active but reluctant to feed at temperatures above 19°C (Elliott 1975a).

The parameter values for the temperature function for rainbow trout were estimated by Rand et al. (1993) based on their analysis of data from From and Rasmussen (1984, Appendix 1) for hatchery rainbow trout. Highest rates of feeding occurred at 20°C. Our estimates for the optimum temperature range differ from those of Rand et al. (1993) and are based on an independent analysis of the From and Rasmussen (1984) data; see Appendix 4 for details. In summary, the f(T) functions for brown and rainbow trout differ substantially, which can differentially affect consumption, especially when water temperature exceeds 18°C.

We note that the parameter estimates for a_{Cmax} and b_{Cmax} and the eight parameters for the f(T) function are based on data for brown trout and rainbow trout greater than 100-mm fork length. The dependence of maximum consumption on body weight and especially on temperature may differ somewhat for fry and juveniles 20 to 100 mm in length (Wismer and Christie 1987).

We impose an additional temperature constraint for all ages of all three species of a critical lower temperature threshold ($T_{crit} = 3.0°C$) below which there is no consumption (and no activity respiration; see Sect. 6.4) (Elliott 1976b, 1984a).

5.6 Nonforaging Option

We include a nonforaging option that is helpful in calibrating and debugging the model and that provides a means of easily evaluating the response of the model to extreme rations, that is, ad libitum feeding and starvation (Elliott 1975d; Brett and Groves 1979). The nonforaging option requires input of constants for the fraction of maximum daily consumption for Age 0 ($F0_{Cmax}$) and for Age 1 and older trout ($F1_{Cmax}$). The constant for Age 0 is generally higher than that for Age 1 and older trout. We use the same values for all three species. When this nonforaging option is used, consumption for each trout (i.e., the C term in eq. 5-1 is calculated each day by multiplying eq. 5-13 by the constant $F0_{Cmax}$ or $F1_{Cmax}$.

SECTION 6 GROWTH: ENERGETIC COSTS

As presented at the beginning of Sect. 5 (eq. 5-1), the bioenergetics model describing the daily growth of individual fry, juveniles, Age 1, and older trout in our model is

$$W(t+1) = W(t) + (1/a_{cal})\,(C - E_{eg} - E_{ex} - E_{SDA} - R), \qquad \text{(eq. 6-1)}$$

where W(t) is the wet weight (g) of the trout on day t, C is energy consumed (cal/day), and the energy losses (all in cal/day) are E_{eg} (egestion), E_{ex} (excretion), E_{SDA} (specific dynamic action), and R (respiration). The constant a_{cal} converts calories of trout to grams wet weight of trout and has a value of 1000 cal/g for Age 0 trout and 1400 cal/g for Age 1 and older trout (Hewett and Johnson 1992). Our representation of consumption (C) is described in Sect. 5. Our representation of energetic costs and changes in length and physiological condition are described in this section.

6.1 Egestion

Egestion (E_{eg}, cal/d) is the energy lost in feces and is represented by using Elliott's (1976c) model for brown trout, with modifications added by Stewart et al. (1983) for their lake trout energetics model (see Hewett and Johnson 1992). Elliott (1976c) developed a model for egestion as a function of temperature (T) and the proportion of maximum ration (W_{eat}/C_{max}, both in grams wet weight). Stewart et al. (1983) provides a correction to account for a mixed diet that includes a proportion of fish (F_{fish}) and not just invertebrates as used in Elliott's (1976c) experiments. Stewart et al. (1983) also consider the indigestible proportion of a prey, which differs for fish prey (X_{fish}) as compared to invertebrate prey (X_{inv}). Because we are assuming an all-invertebrate diet for our current application, the equations in Stewart et al. (1983) simplify to the following equation:

$$E_{eg} = a_{eg}\, T^{b_{eg}}\, \exp(c_{eg}\, W_{eat}/C_{max})\, C\,. \qquad \text{(eq. 6-2)*}$$

We use the same parameter values for all three species, which are taken from Stewart et al. (1983, Table 3; based on Elliott's (1976c) studies on hatchery brown trout).

6.2 Excretion

Excretion (E_{ex}, cal/d) is the energy lost in urine and other secretions (e.g., mucus) and, like egestion, is represented as a function of temperature and proportion of maximum ration, based on Elliott's (1976c) model developed from studies with hatchery brown trout and an adjustment by Stewart et al. (1983) (see Hewett and Johnson 1992). Stewart et al. (1983) adjusted Elliott's (1976c) value for a_{ex} so that excretion is calculated as a fraction of consumption minus egestion, rather than as a fraction of consumption alone. Our equations are

$$E_{ex} = a_{ex}\, T^{b_{ex}} \exp(c_{ex}\, W_{eat}/C_{max})\, (C - E_{eg})\ . \qquad \text{(eq. 6-3)*}$$

We use the parameter values from Stewart et al. (1983) for all three species. Although the sum of energy losses due to egestion and excretion is not as variable as the individual components, it does vary between 10% and 35% of intake, with highest values at intermediate temperatures and high rations.

6.3 Specific Dynamic Action

Specific dynamic action (E_{SDA}, cal/d) is that proportion of a trout's assimilated energy that is used for subsequent biochemical transformation of carbohydrates, lipids, and proteins (and their components) (Brett and Groves 1979). Presumably, SDA is relatively independent of temperature and ration size (Stewart et al. 1983). We represent specific dynamic action as a constant proportion of consumption minus egestion:

$$E_{SDA} = a_{SDA}\, (C - E_{eg}). \qquad \text{(eq. 6-4)}$$

We set $a_{SDA} = 0.14$ (Brett and Groves 1979).

6.4 Respiration

The rate of respiration (R, cal/d) is modeled as the sum of standard respiration (R_{std}) and activity respiration (R_{act}). Our formulation for standard respiration is from Hewett and Johnson (1992) and is a function of the current wet weight of the trout (W) and water temperature (T). Daily activity respiration is represented as a multiple of standard respiration, where the multiple is dependent on the time spent foraging during that day (t_{activ}) and on a factor representing the intensity of activity when foraging (Hewett and

Johnson 1992). We equate this intensity factor to the average velocity experienced by a trout during foraging (V_f, cm/s; see Sect. 5), which is intended to include activity associated with foraging, predator avoidance, and reproductive behavior. The variables t_{activ} and V_f are described in Sects. 5-4 and 5-3, respectively. The value for V_f at this point in a simulation has already been adjusted for body weight and temperature. Our equation is

$$R = R_{std} + R_{act} \text{ , where} \qquad \text{(eq. 6-5)*}$$

$$R_{std} = a_R \, W^{b_R} \exp(c_R \, T) \text{ , and}$$

$$R_{act} = (t_{activ}/24) \, [\exp(d_R \, V_f) - 1.0] \, R_{std} \, .$$

Values for the parameters a_R, b_R, and c_R are not available for Sierra Nevada populations of brown or rainbow trout. Our choice of parameter values has been guided by the species-specific values that are available in the literature (i.e., Elliott 1976b for hatchery brown trout; Dickson and Kramer 1971 and Rao 1968 for rainbow trout) and by Stewart's (1980) review of the literature towards a general model for salmonid metabolism. The parameter d_R is an empirical constant estimated by multiple linear regression (Stewart et al. 1983). We use the same four parameter values for all three species.

We impose the same critical lower temperature threshold (T_{crit}) on activity respiration as we did on consumption (see Sect. 5), under the assumption that when foraging activity is zero, activity respiration is also zero and thus $R = R_{std}$. We set $T_{crit} = 3$°C for all ages of all species.

6.5 Change in Length, Weight, and Condition Factor

The model calculates a new weight for each trout on each day. The length of the trout is updated based on this weight, and then a new condition factor is calculated. Weight-length regression equations of the form $W = a_L \, L^{b_L}$ are available for trout in streams from several sources. Our comparison of these equations made it apparent that considerable variability among populations exists. This finding is not surprising given that trout (especially rainbow) are well known for their phenotypic plasticity and given that they inhabit streams varying widely in factors relating to both energy acquisition and energetic costs. We use the above regression equation in reverse to update the length of each trout:

$$L = (W/a_L)^{(1/b_L)} . \qquad \text{(eq. 6-6)*}$$

Our parameter values for each species are based on several years of data for brown and rainbow trout in Segment 8 of the Tule River, California (T. K. Studley, Pacific Gas & Electric Company, personal communication).

If the length of a model trout on day t is less than that predicted by eq. 6-6 by using the trout's new weight, W(t+1), the trout's length is increased to the predicted length. Otherwise, the length of that trout is not increased and L(t+1) = L(t). The updated value for the condition factor for each trout is calculated as

$$K(t+1) = W(t+1)/a_L\, L(t+1)^{b_L} . \qquad \text{(eq. 6-7)}$$

Note that the maximum value for the condition factor is 1.0. However, whenever a trout loses weight, its condition factor will be less than 1.0, and L(t+1) = L(t).

SECTION 7 HABITAT USE AND MOVEMENT

One goal of this spatially explicit model is to provide a tool to evaluate energetic benefits, energetic costs, and mortality risks for trout that occupy habitats having different velocities, depths, and cover as well as different densities and sizes of trout. The algorithm used here also considers the consequences of having or not having access to a feeding station and to cover.

In developing formulations for processes underlying observed patterns of habitat use and movement, we have kept in mind the space and time scales that we can realistically represent in this model and that we want to represent in this model given our objective (see Sect. 1). Many detailed observational studies have been done on the habitat use and activities of juvenile and adult trout in both streams and lakes, during all seasons including winter and during both day and night (e.g., Angradi and Griffith 1990; Campbell and Neuner 1985; Cunjak 1988; Cunjak and Power 1987; Griffith and Smith 1993; Heggenes et al. 1993; Riehle and Griffith 1993; Riley et al. 1992; Smith and Griffith 1994). While the results from these studies have been invaluable in guiding our approach, the observations are typically at finer space and time scales then we represent in this model. The primary goal of this simulation model is to predict the habitat use, reproduction, growth, and survival of trout over a period of one or more years in response to alternative flow regimes. We do not claim to predict the exact, minute-to-minute location of each trout. Rather, a trout is located each day in a PHABSIM cell within a habitat type with specified characteristics (i.e., depth, velocity, cover, other trout) as a means of simulating flow-related effects on the energetics, movement, spawning, and risks of mortality for that trout. We assume that immigration into and emigration out of the stream segment being modeled balance each other. If data indicate that this assumption is not valid, formulations for emigration and immigration need to be added.

As indicated in the discussion (Sect. 10), one of the primary research needs is the development and testing of a method for characterizing physical habitat of a stream that is designed from the point of view of how the various life stages of fish species in the stream use the physical habitat on a day-by-day basis during different seasons. The spatial grid imposed on a stream by the PHABSIM method of numerous parallel cells that are 1 m or less wide and perhaps 10–100 meters in length does not satisfy this design criterion.

In this section, we describe (1) access to a feeding station, (2) access to instream cover, (3) reasons a model trout might move from its current cell, and (4) how a new habitat unit and cell are selected.

7.1 Access to a Feeding Station

A feeding station (or feeding territory) for a trout in a stream is defined as the area used and defended by a trout while foraging on drift (Grant and Kramer 1990). Typically this territory includes a velocity shelter where the trout holds position between forays to capture prey. On each day we evaluate all trout in a given habitat unit in decreasing order of dominance, keeping track of the cumulative area of feeding stations already held by more dominant trout. Length appears to be the primary determinant of dominance for trout (Keeley and Grant 1993). However, brown trout appear to be more effective at maintaining a feeding station than rainbow trout of comparable length, and hatchery rainbow trout are relatively ineffective at maintaining a feeding station (T. K. Studley, Pacific Gas & Electric Company, personal communication). We quantify this generality by adjusting the actual length (L) of each trout as follows and denote the adjusted length by L_{dom1}:

$$L_{dom1} = v_{spec}\, L \,. \qquad \text{(eq. 7-1)}$$

The parameter v_{spec} is a weighting factor for species. Values for this parameter are adjusted in calibrating the model so that a higher fraction of brown trout than rainbow trout have a feeding station and access to cover and so that most hatchery rainbow trout do not have a feeding station or access to cover. Typical initial values for all ages might be 1.0 for brown trout, 0.9 for rainbow trout, and 0.5 for hatchery rainbow trout. All trout in a given habitat unit are ranked in decreasing order using this adjusted length.

We use Grant and Kramer's (1990) model for area of a feeding station (equals their territory size) versus fork length. The area of a feeding station (A_{stat}, m^2) for a trout of length L (cm) is defined as (Grant and Kramer 1990; see also Godin and Rangeley 1989; McNicol and Noakes 1984; Slaney and Northcote 1974)

$$A_{stat} = a_{stat} L^{b_{stat}} , \qquad \text{(eq. 7-2)}$$

where $a_{stat} = 0.00148$ and $b_{stat} = 2.61$ (Grant and Kramer 1990). Values of A_{stat} are multiplied by a scaling factor (c_{stat}), the value of which is determined separately for Age 0 and for older trout in calibrating the model to ensure that a reasonable percentage of trout have feeding stations. We use the same parameter values for all three species. When addition of the area of a feeding station required by the next model trout exceeds the cumulative wetted area of the habitat unit already allocated on that day (A_{HU}), that next trout does not have access to a feeding station in its current habitat unit and feeds on benthos (Sect. 5).

At extreme temperatures trout seek instream cover and thermal refuges, and feeding stations become irrelevant. We assume that feeding stations are not a contested resource when temperature is below a minimum threshold (T_{tmin}) or above a maximum threshold (T_{tmax}). Our estimates for these two temperature parameters are (6.0°C, 19.0°C) for brown trout and (8.0°C, 21.0°C) for rainbow trout (Campbell and Neuner 1985; Heggenes et al. 1993; Riehle and Griffith 1993).

7.2 Access to Instream Cover

The type and amount of cover in a stream is typically of critical importance in influencing the daily dynamics of fish in streams (see references cited in the introduction to this section). The types of cover include instream cover (e.g., boulders, logs), undercut banks, overhead cover, and surface turbulence. Cover is important in providing velocity shelters for feeding and resting as well as refuges from predators. In this model we consider only instream cover. Estimates of the percentage of instream cover (F_{cov}) at a reference flow are available for each of the habitat units in Segment 8 of the Tule River (Studley et al. 1995). We use these estimates in our formulation for drift foraging (Sect. 5) and the associated activity respiration (Sect. 6), in which case we assume the cover is being used as a velocity shelter, and in our formulation for risk of mortality due to predation (Sect. 8), in which case we assume the cover is being used as a refuge from predators.

In the stream, competition for instream cover (e.g., boulders, logs) is distinct from competition for feeding stations, but is represented in a similar manner. On each day, we process all trout in a given habitat unit in decreasing order of dominance, keeping track of the cumulative area of cover held by more dominant trout. As with feeding stations, size appears to be the primary determinant of dominance for trout. However, brown trout appear to have a higher relative preference for cover (F_{cov}) than rainbow trout (T. K. Studley, Pacific Gas & Electric Company, personal communication). We quantify this generality by adjusting the actual length (L) of each trout as follows and denote the adjusted length by L_{dom2}:

$$L_{dom2} = v_{spec}\, L \;. \qquad \text{(eq. 7-3)}$$

The parameter v_{spec} is the same weighting factor for species described for eq. 7-1. Values for this parameter are adjusted in calibrating the model so that a higher fraction of brown trout than rainbow trout have cover and so that most hatchery trout do not have cover. All trout in a given habitat unit are ranked in decreasing order, by using this adjusted length.

We simulate each trout's access to instream cover such as boulders and woody debris. For each habitat unit we have an estimate at baseflow of the fraction of the bottom area having instream cover (F_{cov}; Studley et al. 1995, Table 4.2-1 and raw data from PG&E); we assume that this fraction applies at all flows. The total area of instream cover for each habitat unit (A_{HUcov}, mm^2) is estimated as

$$A_{HUcov} = f_{cov}\, F_{cov}\, A_{HU} \;, \qquad \text{(eq. 7-4)}$$

where A_{HU} is the wetted area of a habitat unit (which can change daily with flow), and f_{cov} is a scaling factor that is adjusted in calibrating the model to assure that the majority of trout at an average density of trout have access to cover.

In the model, we use length of cover (L_{cov}, mm), rather than area, to characterize the size-frequency distribution of cover objects. We represent the length-frequency distribution of cover objects [$f(L_{cov})$] as an exponential distribution, assuming that there are many small cover objects and few large cover objects

$$f(L_{cov}) = \exp(-L_{cov}/\bar{L}_{cov}) \;. \qquad \text{(eq. 7-5)}$$

The parameter $\bar{L}_{cov}$ is the median length (mm) of cover objects in a habitat unit. The value of this parameter is adjusted during model calibration to assure that the majority of trout at an average density of trout have access to cover. As an example, a value of $\bar{L}_{cov} = 60$ mm for the Tule River appears to achieve this calibration requirement. Further study is required to operationally test this formulation.

This length-frequency distribution for instream cover objects is divided into two nonoverlapping parts. The first part is the length-frequency distribution for small cover objects that are usable by small trout, which we define as all Age 0 trout. The second part is the length-frequency distribution for the large cover objects that are usable by large trout. We define large trout as Age 1 and older brown and rainbow trout and all hatchery rainbow trout. (Even though hatchery trout are stocked at Age 0, they are larger than most Age 1 brown and rainbow trout.) This separation is motivated in part by the observation that cover large enough for large trout may not serve as refuge for small trout because of risk of predation by large trout. Each small trout that obtains access to cover in the model removes an area of cover equal to the square of its length from the total area of instream cover still available to small trout in that habitat unit. A similar condition applies for each large trout that obtains access to cover. As an example, a small trout of length L has access to instream cover in its current habitat unit on a given day if

$$L^2 \leq A_{HUcov} \, [\exp(-L/f_{cov}) - \exp(-L_{small}/f_{cov})] - \Sigma L^2 \, , \qquad \text{(eq. 7-6)}$$

where the final term in this equation is the cumulative area of cover already assigned to more dominant small trout on that day. A similar equation applies for large trout. When addition of the area of instream cover required by the next model trout exceeds the area of cover remaining to be allocated, that trout does not have instream cover in its current habitat unit on that day for either a velocity shelter or a refuge.

7.3 Decision to Move

All trout are given the opportunity to move each day. Movement is implemented at the start of each day, but may be based on what a trout experienced on the previous day. A model trout departs from its current cell for either of two reasons: (1) the cell is not physically habitable or (2) the ratio of mortality risk to growth is greater than expected. The model can be run using either or both of these criteria. In addition, a low daily probability exists of a trout moving from its current cell for unspecified reasons (P_{move}) (i.e., stochastic movement).

7.3.1 Cell Is Not Physically Habitable

A model trout is given the opportunity to move from its current cell if the cell is no longer physically habitable because of changes in flow. The two criteria of not being habitable are (1) the depth is less than d_{move} times the length of the trout and (2) the average water column velocity is greater than the maximum swimming speed (see Sect. 5). The value for d_{move} may be adjusted in calibrating the model, but a reasonable value is 1.0.

7.3.2 Ratio of Mortality Risk to Growth

A model trout alive on day t is given the opportunity to move from its current cell at the start of that day if on the previous day the ratio of mortality risk to growth for that trout was greater than expected (Tyler and Rose 1994). The stream segment being modeled can be viewed as a two-dimensional surface of mortality risk and growth potential that changes over time in response to changes in flow, mortality risks, and prey availability. We assume that each trout moves with the goal of minimizing the ratio of mortality risk to growth potential (i.e., u/g; Werner and Gilliam 1984), but that it is constrained by the amount of information that it has about the surrounding environment. We assume that the fish has a sense of the risks of mortality and of its energetic status. We treat the different risks of mortality as independent probabilities and calculate a daily probability of mortality due to all causes (P_{tot}) as

$$P_{tot} = \prod(1.0 - P_i) \, , \qquad \text{(eq. 7-7)}$$

where the P_i values are for each of the risks of mortality discussed in Sect. 8, including fishing mortality (P_{fish}). Daily growth in weight (ΔW) is used as an integrated measure of energy intake and metabolic cost. We assume that a trout forms an expectation of mortality risk (P^*_{tot}) and an expectation of energetic status (ΔW^*) that is simulated as a running average of the ratio ($P^*_{tot}/\Delta W^*$) of each trout's unique history of mortality risks and growth, weighted by a memory factor (f_{mem}) (Berstein et al. 1988, 1991):

$$P^*_{tot}(t)/\Delta W^*(t) = f_{mem}\ P^*_{tot}(t-1)/\Delta W^*(t-1) + (1.0 - f_{mem})\ P_{tot}(t-1)/\Delta W(t-1)\ . \qquad \text{(eq. 7-8)}$$

Our u/g departure rule allows a fish to move when conditions for survival and growth in the current location are below expectation. A model fish departs its current cell on the next day if the expected ratio of mortality risk to growth on day t is greater than the expected (Charnov 1976) [i.e., if $P_{tot}(t)/\Delta W(t) > P^*_{tot}(t)/\Delta W^*(t)$].

7.4 New Cell and Habitat Unit

Selection of a new cell and habitat unit reflects a behavioral strategy of minimizing the risk of mortality by not selecting a cell that is too shallow or that has a velocity that is too high. Unlike making the decision to move, however, the selection process does not reflect a behavioral strategy of maximizing growth potential. If a model trout has an opportunity to move from its current cell because the the cell is not physically habitable or the ratio of mortality risk to growth is greater than expected, other cells in the current habitat unit are sampled according to the following algorithm. For a habitat unit with N cells, the model trout has N chances to select a cell at random (with replacement). The first cell selected that has adequate water depth (i.e., $D \geq d_{move}\ L$, where L is the length of the trout) and velocity (i.e., $V_{ave} \leq S_{max}$) is assigned to the trout. In a model with spatial variation in temperature among cells within a habitat unit, temperature in the cell would also have to meet trout tolerances.

If no habitable cell is found within the trout's current habitat unit, then adjacent habitat units are evaluated. The habitat unit is selected by evaluating the adjacent unit that is reachable (i.e., no impassable cascade). The direction (upstream or downstream) is chosen at random for juvenile and older trout, it is always downstream for fry (Heggenes and Traaen 1988), and is always upstream the day a trout spawns. The above algorithm for selecting a habitable cell is used in the new habitat unit. If this unit is rejected, the search continues in the unit adjacent to the original habitat unit but in the opposite direction. If this new unit also is rejected, the trout remains in the original habitat unit and cell. This formulation allows trout to move out of a unit that is not habitable in terms of water depth and velocity and also allows us to predict the change in habitat use with age and size of trout. For computational simplicity, we restrict movement to one habitat unit per day.

SECTION 8 MORTALITY

Each trout in the model is exposed daily to mortality risks that depend on its attributes, such as length and physiological condition, and on local habitat conditions, such as velocity and cover. This section is divided into the following subsections: (1) Natural Mortality, (2) Fishing Mortality, and (3) Mortality of Hatchery Rainbow Trout.

8.1 Natural Mortality

We consider the following natural mortality risks for each trout: (1) high temperature, (2) high velocity, (3) stranding, (4) spawning, and (5) physiological condition, length of the trout, and daily period of activity.

8.1.1 High Temperature

High temperature can directly result in mortality. Age 1 and older of both species are less temperature tolerant than Age 0 (personal communication, C. C. Coutant, Oak Ridge National Laboratory, Oak Ridge, TN). We use the following daily temperature thresholds above which a model trout is dead: 24.0°C for Age 0 and 20.0°C for older brown trout, and 26.0°C for Age 0 and 22.0°C for older rainbow trout (Bidgood and Brett 1969; Coutant 1970; Elliott 1994). These estimates are not based on data for trout from Sierra Nevada streams.

8.1.2 High Velocity

When faced with the risk of being swept downstream, a trout moves to the bottom and other areas of low velocity (Sect. 7). All trout are given the opportunity to move at the start of each day. One reason for moving from one cell to another is that the velocity in its current cell is too high. Once movement has been accounted for, we determine whether each model trout has access to cover or not (Sect. 7). If a trout has access to cover in its current cell, it is protected from being swept downstream on that day. If a trout does not have access to cover, we compare the average water column velocity (V_{ave}) in the trout's cell to the trout's maximum swim speed (S_{max}) (Sect. 5). If $V_{ave} > S_{max}$, the trout dies from being swept downstream. We do not currently include an option for a trout that is swept downstream to find a shelter in some downstream habitat unit.

8.1.3 *Stranding*

As mentioned in discussing mortality due to high velocity, each trout is given the opportunity to move at the start of each day. One reason for moving from one cell to another is that the depth of the current cell is too shallow. A trout will attempt to leave its current cell if the depth (D) is less than some fraction of the length of the trout (i.e., $D < d_{move} L$); we set d_{move} at 1.0 for all life stages of all three species (Sect. 7). If a trout is unable to move from a cell that is too shallow because that cell is surrounded by cells having zero depth, that trout is stranded and is subjected to a daily risk of mortality because of stranding (P_{strand}) on each day that $D < d_{die} L$. We set $P_{strand} = 0.5$ and $d_{die} = 0.2$ for all life stages of all three species.

8.1.4 *Mortality Associated with Spawning*

We assign a risk of mortality (P_{repro}) to each female and male trout that spawns. Age 2 and older rainbow trout experience higher mortality than Age 2 and older brown trout (Studley et al. 1995), suggesting that mortality associated with reproduction may be higher for rainbow trout than brown trout. In calibrating the model, our species-specific values for P_{repro} are selected to help achieve the observed densities of brown and rainbow trout. The parameter P_{repro} could be made a function of size or age of the trout. Each mature female experiences this one-time risk of mortality on the day she spawns. Because we do not model the day of spawning by males, each mature male is assigned a day at random from the calendar-date spawning window for that species (see Sect. 3.2), and he experiences this one-time risk of mortality on that day. This assignment is done assuming each day is equally likely for each male. For each female and male, a number is selected at random from a uniform [0, 1] distribution; if this number is $\leq P_{repro}$, the trout dies.

8.1.5 *Physiological Condition, Length of Trout, and Daily Period of Activity*

We make the following assumptions concerning risks of natural mortality, in addition to the four risks explicitly represented above. First, risks of natural mortality can be divided into two categories, those that are present 24 h a day every day (e.g., disease, parasites) and those that are present primarily when a fish is active (e.g., predation). We assume that all mortality risks are greater (1) for a fish in poor versus good physiological condition and (2) for a small versus a large fish. In addition, a fish cannot survive when its physiological condition decreases to some minimum. Based on these assumptions, we represent the daily probability of mortality (P_{mort}) as follows:

$$\begin{aligned} P_{mort} &= 1.0 \,, & K \leq K_{min} \,, \qquad & \text{(eq. 8-1)*} \\ &= 1.0 - \exp(-Z) \,, & K_{min} < K \leq 1.0 \,, \qquad & \end{aligned}$$

$$\text{where } Z = F_K \, F_L \, [Z_{24} + (t_{activ}/24) \, Z_{act}] \,.$$

The factor F_L is defined as (Fig. 8-1)

$$\begin{aligned} F_L &= 1.0 \,, & L \leq L_{min} \,, \qquad & \text{(eq. 8-2)*} \\ &= 1.0 + a_M \, (L - L_{min}) \,, & L_{min} < L < L_{max} \,, \qquad & \\ &= F_{Lmax} \,, & L \geq L_{max} \,, \qquad & \end{aligned}$$

$$\text{where } a_M = (F_{Lmax} - 1.0)/(L_{max} - L_{min}) \,.$$

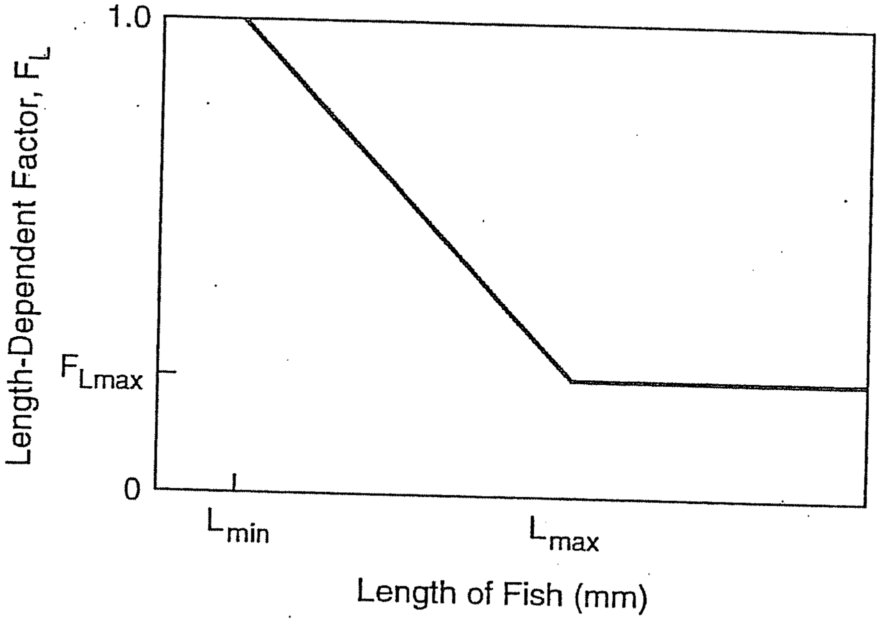
The factor F_K is defined as

$$\begin{aligned} F_K &= (1.0 - K_{min})/(K - K_{min}) \,, & K_{min} < K < 1.0 \,, \qquad & \text{(eq. 8-3)*} \\ &= 1.0 \,, & 1.0 \leq K \,. \qquad & \end{aligned}$$

The daily instantaneous mortality rate (Z) is the sum of the instantaneous mortality rate for those risks present 24 hours a day (Z_{24}) and the instantaneous mortality rate for those risks present primarily when a fish is active (Z_{act}); values for these two parameters are selected in calibrating the model. The term $t_{activ}/24$, which can vary each day for each trout, is the fraction of a day a model trout is active (see Sect. 5-4). We assume that vulnerability to predation depends on whether or not a trout has ready access to instream cover as a shelter from predation during its daily period of activity. If cover is not available, the variable $t_{activ}/24 = 1.0$, implying that the trout is vulnerable to predation 24 hours a day.

The length-dependent factor (F_L) is a straight line with a negative slope. Risks of mortality represented by both Z_{24} and Z_{act} are assumed to decrease as length increases. The slope (a_M) is that of a line connecting the two points (L_{min}, 1.0) and (L_{max}, F_{Lmax}). For all three species

Fig. 8-1 Length-dependent factor in the equation for the daily probability of natural mortality, P_{mort} .



we fix L_{min} at 20 mm (the minimum length of a fry upon emergence from a redd; see Sect. 4), and we fix L_{max} at 200 mm. The value for F_{Lmax} is between 0.0 and 1.0 and is interpreted as the relative decrease in risks of natural mortality for a large fish (L_{max}) compared to a small fish (L_{min}) for which the length-dependent factor has a value of 1.0 (see Appendix 4). The value for F_{Lmax} is selected in calibrating the model.

The condition-dependent factor (F_K) has a value of 1.0 when K = 1.0, which is the maximum value for K (Sect. 6). This ratio becomes a large number as K decreases toward K_{min}, in which case P_{mort} approaches 1.0, which satisfies the constraint that a fish dies when $K = K_{min}$ (see Appendix 4). We view K_{min} as an autoecological threshold for our index of physiological condition (i.e., it is independent of the external abiotic and biotic environment). When K of a model trout decreases to this threshold, the individual is lost to the population, whether because of predation, disease, passive emigration downstream and out of the stream segment, or other proximate cause. From Elliott (1984b) we calculated the condition factor (a W^b/L^3) of downstream-moving fry in spring and summer, many of which were in noticeably poor condition. The condition factor was 0.50 for trout ≤ 40 mm amd 0.67 for trout > 40 mm. Although we have no data for estimating condition factor for Age 1 and older trout in noticeably poor condition, Shuter et al. (1980) indicates that condition factors in the range 0.4–0.6 are typical for many trout and other species under starvation conditions just before death. We use K_{min} = 0.5 for all ages of the three species.

If justified by the data for a specific stream, Eq. (8-1) can be modified to represent predation, including cannibalism. Piscivory is well-documented in the literature for stream populations of brown trout (Alexander 1977), but it is relatively uncommon for stream populations of rainbow trout. McCormack (1962) found brown trout eggs and alevins in the stomachs of brown trout over 10 cm (Age 2 and older). He also mentions observations by others of trout attacking emerging alevins. Only a very limited number (< 0.1%) of instances of trout in the stomachs of large trout have been observed in the Tule River (Studley et al. 1995, pp. 4–147 and Table 4.4-10).

Risk of predation and predator avoidance depend on the type of predator (e.g., fish, snake, bird, terrestrial mammal) and on the availability of different types of cover (e.g., instream boulder or debris, undercut banks, overhead vegetation, water surface turbulence). Given this generality, there are two fundamental problems that have led us to the decision to not attempt to represent predation and predator avoidance in a detailed mechanistic manner. First, data are not available for the Tule River (or any other stream) on types, numbers, or relative effectiveness of predators (other than large trout; see above). Second, although limited data are available for the Tule River on the availability of different types of cover (as percentages for each habitat unit), the scale of spatial and temporal resolution required to mechanistically represent predator avoidance is finer than the scale of PHABSIM cells and the daily time step that we use in this model.

In summary, Eq. (8-1) incorporates what we feel are the main factors regulating the risk of natural mortality in addition to those discussed in Sects. 8.1.1 through 8.1.4. A trout has a higher daily probability of mortality when it is in poor condition, when it is small, when it is active, when it does not have access to cover, and when there are more predators (Fig. 8-1).

8.2 Fishing Mortality

We represent fishing mortality in considerable detail because it is a major source of mortality, data are commonly available to guide an appropriate formulation, and fishing mortality is potentially density dependent. We specify a maximum daily probability of fishing mortality (P_{fmax}) corresponding to conditions that would maximize the number of trout killed by anglers. We adjust this maximum with a series of independent multipliers, each of which is restricted to the range [0.0, 1.0]. Our equations are as follows:

$$P_{fish} = [f_{keep} + (1.0 - f_{keep})\, f_{hook}]\, P_1 \text{ , where} \qquad \text{(eq. 8-4)}$$

$$P_1 = f_{day}\, f_{month}\, f_{spec}\, P_2 \text{ .}$$

In turn,

$$P_2 = f_{dens}\, P_{fmax} \text{ , where} \qquad \text{(eq. 8-5)*}$$

$$f_{dens} = \exp(N)/[1.0 + \exp(N)] \text{ .}$$

The various parameters in these equations will now be defined.

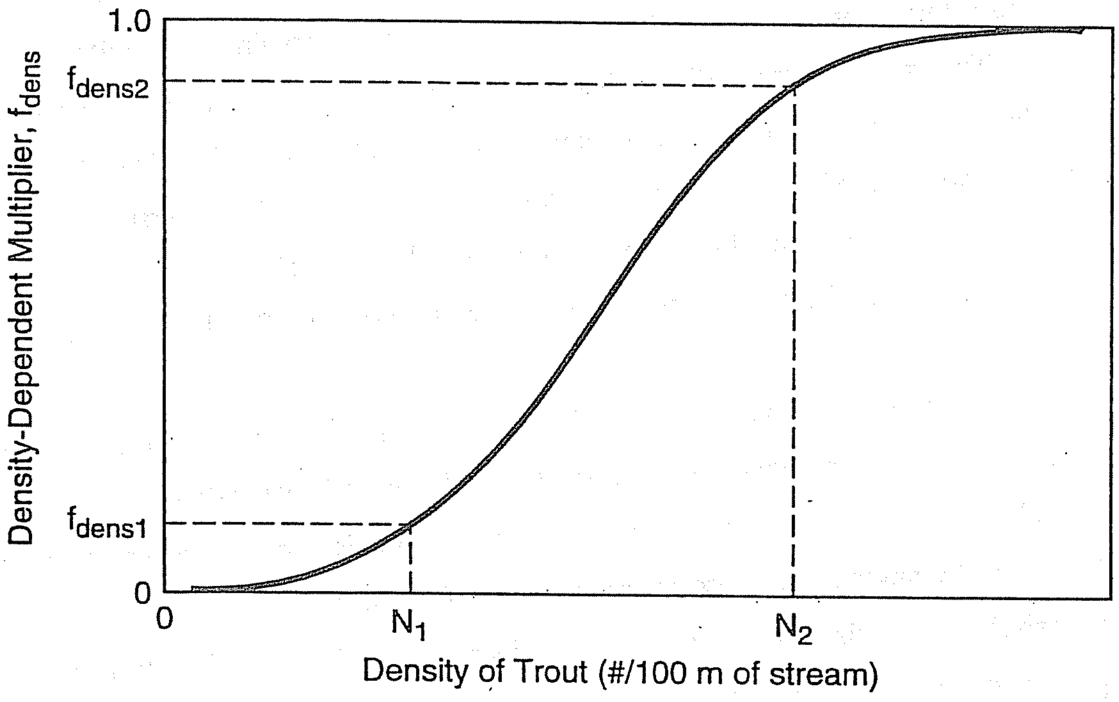
Currently, no number or length limits for trout caught in the Tule River exist. Thus, we assume in the model (1) that all Age 1 and older brown trout and rainbow trout and all hatchery rainbow trout are legally catchable and (2) that anglers key to the combined density of all legally catchable trout of these three "species" (N in eq. 8-5). An alternative assumption would be that anglers key primarily to the density of hatchery rainbow trout, because fishing effort (as hours fished) is better correlated with catch of hatchery trout (as number kept per 100 m of stream) than with catch of wild trout (Studley et al. 1995, Sect. 4.4.1 and Appendix N). N is updated in the model at the start of each day to include new stocking of hatchery rainbow trout on that day and mortality of trout of each of these three species during the preceding day. With little effort the definition of N could be modified to include length limits.

The maximum daily probability of fishing mortality (P_{fmax}) corresponds to conditions that would maximize the number of trout killed by anglers. On the basis of data for the Tule River, these conditions in the model are a density of 200 or more trout per 100 m of stream, a weekend day in June, and no trout caught by anglers are released. Our initial estimate for P_{fmax} is 0.05. This value corresponds to a probability of fishing mortality for a hatchery rainbow trout of 0.5 during the 14 days following stocking, which reflects the opinion of PG&E and ENTRIX staff working in the Tule River that more than half of the trout stocked on a given day are gone within 2 weeks. An analysis of the stocking and creel-census data indicates that ~50% of the hatchery rainbow trout stocked during the season are caught by anglers.

The history of stocking hatchery trout in the United States and other countries clearly indicates that fishing effort and mortality increase whenever and wherever stocking occurs (Moring 1993; Vincent 1987). Thus, we represent the density-dependent multiplier (f_{dens}) as a logistic function of the density of trout. This function approaches 0.0 at low values of N and 1.0 at high values of N (Fig. 8-2). We require that this function pass through the two points (N_1, f_{dens1}) and (N_2, f_{dens2}). The values for these four coordinates are selected based on a combination of empirical data and expert judgement. Our values are (100 trout/100 m, 0.20) and (200 trout/100 m, 0.95). The 100 trout/100 m is approximately equal to the average density of Age 1 and older brown and rainbow trout in Segment 8 of the Tule River. The 200 trout/100 m is double this average density and allows for stocking of hatchery rainbow trout at levels higher than currently used. The Y-axis coordinates for these two densities (i.e., 0.20, 0.95) are selected to ensure that the function for f_{dens} covers nearly all the range between 0.0 and 1.0.

We include multipliers of P_{fmax} to represent the differences in fishing effort between days within a week (f_{day})and between months (f_{month}). The creel-census data indicate that the daily probability of fishing mortality is higher on weekend days than weekdays and is higher during June than the other 5 months of the fishing season (Studley et al. 1995, Appendix N). We calculated relative values between 0.0 and 1.0 from these data. We use $f_{day} = 1.0$ for Fridays, Saturdays, Sundays, and the three holidays (Memorial Day, July 4th, and Labor Day), and $f_{day} = 0.85$ for all other days. Fishing effort (approximated as number of anglers multiplier by the average number of hours fished per angler) is higher on the weekends, due primarily to the number of anglers being higher,. even if the average number of hours fished is somewhat lower. Also, skilled anglers, although more likely to fish on weekdays and catch more trout, are more likely to release any trout they catch. Our values for f_{month} are 0.2 (April), 0.8 (May), 1.0 (June), 0.8 (July), 0.6 (August), and 0.2 (September) (Studley et al. 1995, Figure 4.4-1C). These multipliers for days and months are applied each day of the fishing season. The average beginning and end dates (J_{fish1}, J_{fish2}) for the fishing season in the Tule River are currently April 27 and September 30, where on average April 27 corresponds to the last Saturday in April.

Fig. 8-2 Density-dependent multiplier of fishing mortality as a logistic function of the combined densities of brown, rainbow, and hatchery rainbow trout. Fishing is a potential density-dependent source of mortality that may compensate for changes in other sources of mortality, resulting in stabilization of a trout population.



A comparison of the proportions of trout caught in the Tule River that are brown trout, rainbow trout, or hatchery rainbow trout (compared to the densities of these three groups in the stream) clearly indicates that hatchery rainbow trout are much more vulnerable to fishing mortality than brown trout or rainbow trout. Of the trout caught in Segment 8, more than 90% are hatchery rainbow trout. The catching of brown trout and rainbow trout may be an incidental by-catch, although there are undoubtedly some "pure" anglers who direct their fishing effort at brown trout and rainbow trout and want nothing to do with hatchery rainbow trout. The greater vulnerability of hatchery rainbow trout is due both to characteristics of the hatchery rainbow trout (e.g., naive about predators including anglers, tendency to school) and to characteristics of the anglers (e.g., using canned corn on a hook versus a fly resembling the currently dominant invertebrate species in the drift). Our values for f_{spec} are 1.0 for hatchery rainbow trout, 0.2 for rainbow trout, and 0.1 for brown trout (Studley et al. 1995, Fig. 4.4-9).

Based on data from PG&E, the probability that a caught trout is kept (f_{keep}) is ~0.8, and the probability that a trout that is caught and then released subsequently dies from hooking mortality (f_{hook}) is 0.1. The same values apply to all model trout. We keep track separately of trout kept by anglers and those released that die from hooking mortality. Undoubtedly the probability that a fisher keeps a given trout increases as the size of the trout increases. If this issue is deemed important, as it might be for a trophy fishery, f_{keep} could be made a function of length. Another aspect of fishing mortality that could be considered is that hooking mortality is greater for live versus artificial bait and for barbed versus barbless hooks.

In summary, we have the following formulation for the daily risk of fishing mortality (P_{fish}):

$$P_{fish} = [f_{keep} + (1.0 - f_{keep})\, f_{hook}]\, P_1 \text{ , where} \qquad \text{(eq. 8-4)}$$
$$P_1 = f_{day}\, f_{month}\, f_{spec}\, P_2 \text{ .}$$

In turn,

$$P_2 = f_{dens}\, P_{fmax} \text{ , where} \qquad \text{(eq. 8-5)*}$$
$$f_{dens} = \exp(N)/[1.0 + \exp(N)] \text{ .}$$

This formulation reflects the types of data available for the Tule River (Studley et al. 1995). The approach, however, is easily modified for any other site or simplified if certain types of data are not available.

8.3 Mortality of Hatchery Rainbow Trout

Most hatchery rainbow trout stocked in mountain streams, like the Tule River, do not survive for more than a few weeks (Moyle 1976; Studley et al. 1995). Both fishing and risks of natural mortality take a heavy toll because hatchery trout are naive about predators (including anglers) and do not effectively compete with native trout for space and food. All of the risks of mortality described in this section apply to hatchery rainbow trout. Only fishing mortality, however, includes a species-specific factor for vulnerability (f_{spec}). To independently control the mortality rate of hatchery rainbow trout and reflect the observation that most hatchery rainbow trout survive for only 1–2 weeks, a daily risk of mortality which applies only to hatchery trout is calculated. We assume that the six risks of mortality that apply to all trout, including fishing, are independent of each other in a probabilistic sense (i.e., they are competing sources of mortality). Each hatchery trout is subjected to that day's risks of mortality, that is, (1) high temperature, (2) high velocity, (3) stranding, (4) mortality associated with spawning, (5) condition, length, and period of activity, and (6) fishing. Then each surviving hatchery trout is subjected to an additional daily risk of natural mortality (P_{HRT}) calculated as

$$P_{HRT} = 1.0 - [PS_{HRT}/(1.0 - P_1)(1.0 - P_2) \ldots (1.0 - P_6)] \, , \qquad \text{(eq. 8-6)}$$

where PS_{HRT} is the expected daily probability of survival for a hatchery rainbow trout. The value of the parameter PS_{HRT} is determined in calibrating the model. As an example, if we assume that the probability of a hatchery trout surviving for 2 weeks is 0.1, this corresponds to a daily probability of survival of 0.848.

SECTION 9 MODEL CALIBRATION

Calibration is an imperfect science. Focusing on simple end points that reflect isolated processes, such as consumption, is the best way to reduce the number of assumptions and the uncertainty in parameter estimates (Table 9-1). However, complex end points that reflect the integration of many isolated processes, such as length and abundance of fish, are also important. Although quantitative end points are always desirable, semiquantitative end points (e.g., inequalities) and qualitative end points are also used in calibrating a simulation model.

Table 9-1. Four types of calibration and examples of each

Calibration Type	Simple	Complex
Qualitative	Mixture of foraging strategies	Larger trout use pools more than small trout
Quantitative	Development rate of eggs & alevins Consumption	Length Abundance Habitat use

Bart (1995) proposed several criteria for the calibration of an individual-based simulation model that should be satisfied prior to using the model to address management issues. One of his criteria is that model predictions and field observations should be in reasonable agreement for the baseline or reference case. This section compares historical model "predictions" (hindcasts) with field observations from the Tule River during 2 years which had contrasting stream flow (Fig. 9-1) and temperature (Fig. 9-2) regimes. The section of the Tule River below the Tule River Diversion Dam was characterized by low, stable flows and warm temperatures during water year 1988 (October 1, 1987 to September 30, 1988). In contrast, stream flows in water year 1991 were both higher and more variable (except during the summer) as well as often being accompanied by lower water temperatures. Several major floods occurred in water year 1991 and temperatures warmed slower in the spring than normal.

Fig. 9-1. Stream temperature recorded below the Tule River Diversion Dam for water years 1988 and 1991.

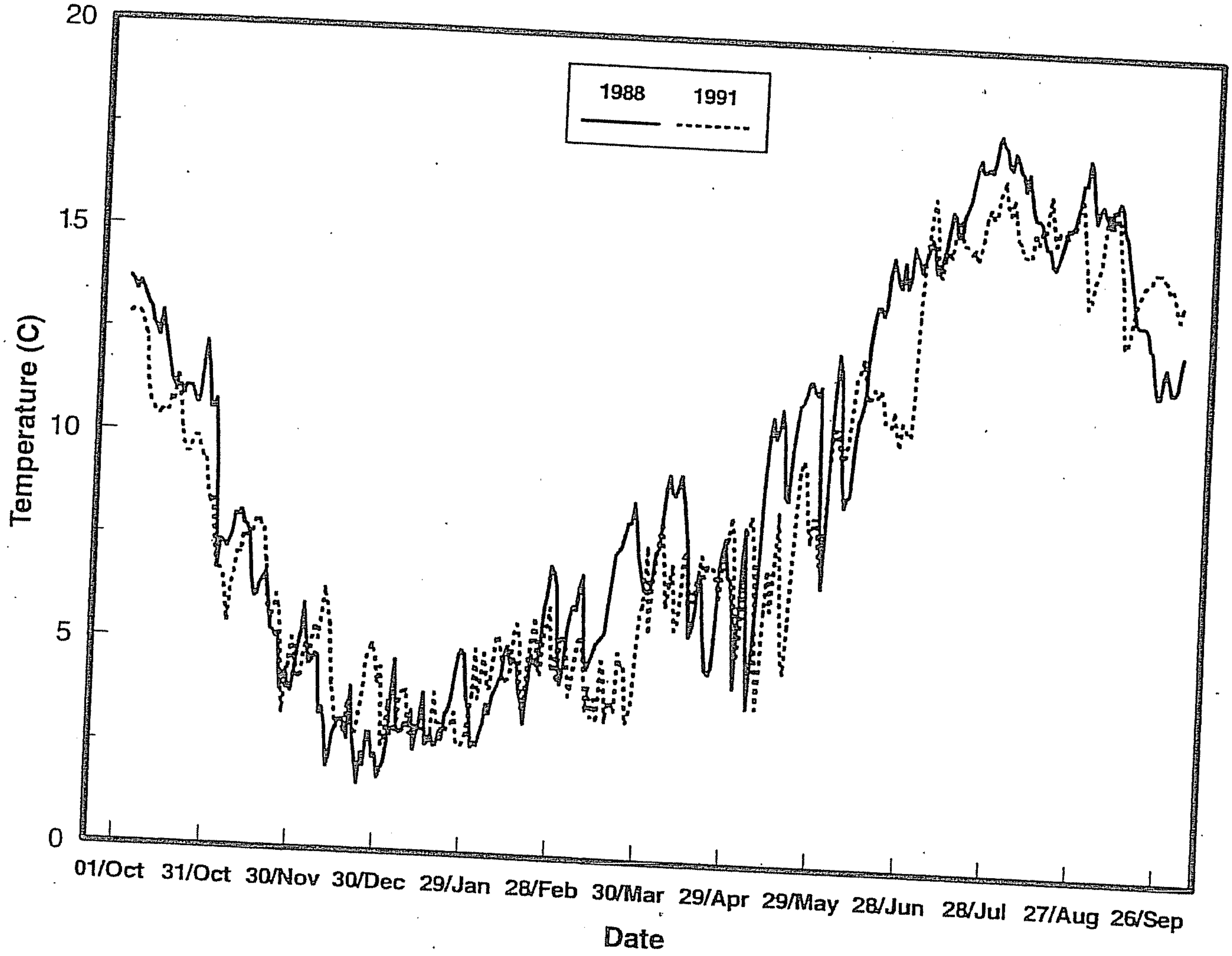
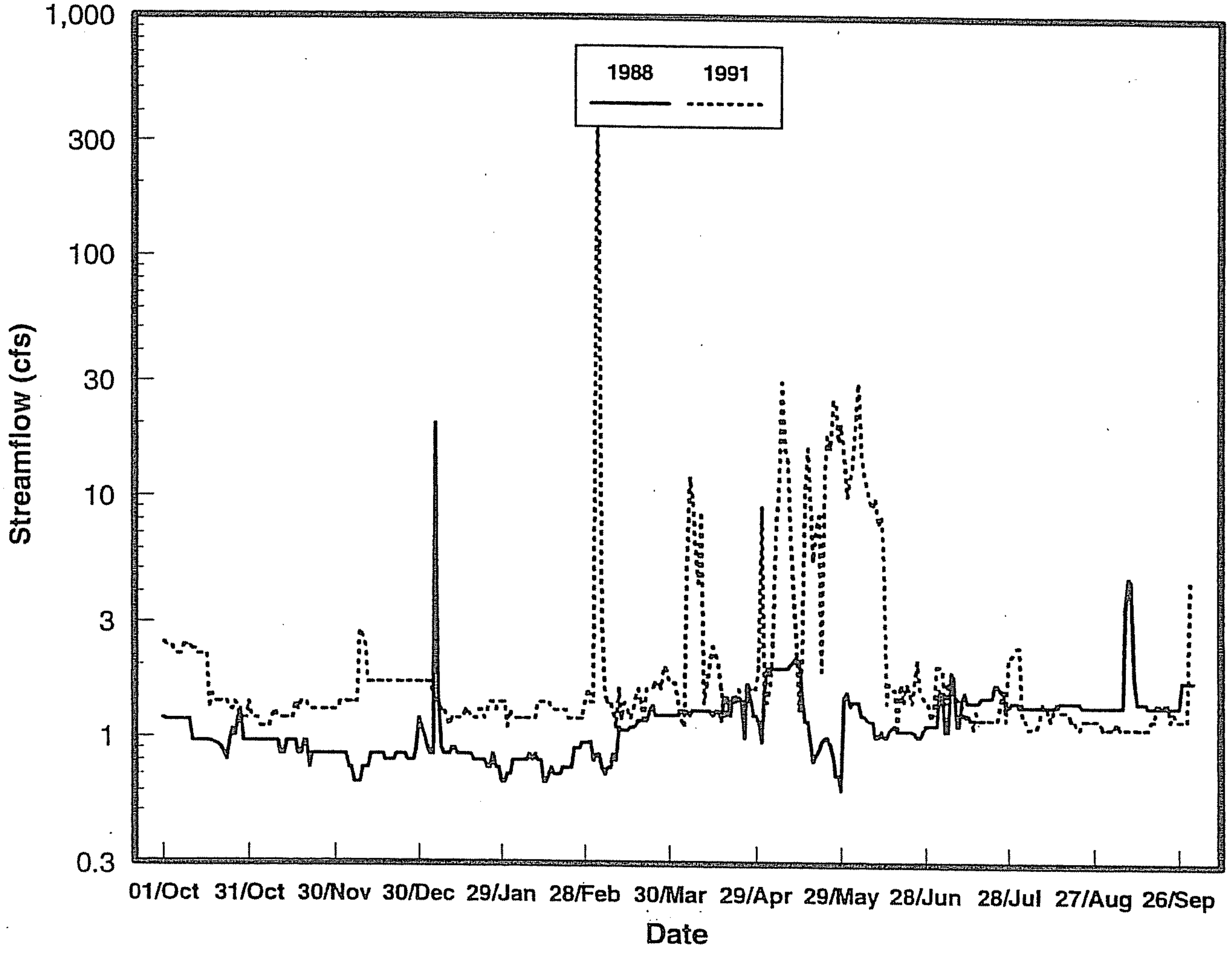


Fig. 9-2. Stream flow recorded below the Tule River Diversion Dam for water years 1988 and water year 1991.



Our three primary calibration efforts involved matching predicted to observed (1) length distributions, (2) abundances, and (3) habitat use. To some extent these can be done independently. However, density-dependent factors may influence growth and habitat use, and size-selective mortality can result in shifting length distributions over time. Parameter values used in these simulations are given in Appendix 1. The site-specific data to which we have compared model results are from the Altered Flows Project for Segment 8 of the North Fork Middle Fork Tule River, California (Studley et al. 1995).

9.1 Site-Specific Initial Conditions

To make use of the annual fall population survey results for initial conditions (Studley et al. 1995), each simulation started on October 1 . We defined the initial number, age composition, and length and weight distributions of brown and rainbow trout populations in the model on the basis of data from fall population surveys in Segment 8 of the Tule River (Appendix 5, Table A5-3). The initial length of each trout was selected at random from a triangular distribution with a mode equal to the average length measured in the Tule River for that age and species. The weight (W) of each trout is

$$W = a_L L^{b_L} + z W_{SE} , \qquad (9\text{-}1)$$

where a_L and b_L are the parameters relating expected wet weight of a trout to its length, W_{SE} is the average error associated with the prediction of weight from length, and z is a standard normal deviate. The sex ratio in the initial Age 1 and older cohorts was 1:1.

Each trout was initially located in a habitat unit. The exact location was not important because the trout have an opportunity to move, even on the first day of the simulation. We assigned Age 1 and older trout to pool habitat units. We assigned all Age 0 trout to pool, run, pocket water, and riffle habitat units. In all cases, we adjusted for the length of each habitat unit so that the initial density was the same in each habitat unit.

We stocked hatchery rainbow trout in the model in such a way as to approximate actual stocking rates. The model added N_{stock} hatchery rainbow trout every t_{stock} days during the stocking season (t_{stbeg} through t_{stend}). Trout were stocked at a length of L_{stock} and a weight of

W_{stock} . For the Tule River, we add 300 model hatchery rainbow trout every 7 days from April 25 through August 27; each trout is 250 mm long and 200 g wet wt (Judy Urrutia, California Department of Fish and Game, personal communication). This results in 18 days of stocking and a total of 5400 hatchery rainbow trout stocked per year. Hatchery rainbow trout were added to each pool habitat unit in proportion to the length of the habitat unit.

9.2 Calibration of Growth

Trout growth is controlled by the balance between energy intake and energy costs. In the absence of site-specific data on energy costs, we assumed that energy costs were accurate and focused on energy intake during calibration. We used three end points. First, we had access to site-specific stomach data for both Age 0 and adult trout; these data provided guidelines for calibrating foraging intake. Second, we balanced the availability of drift and benthic prey to ensure that a mixture of foraging modes was employed by model trout, as is usually observed in the field. Third, we adjusted parameter values relating to foraging to ensure that simulated annual growth of trout agreed with observed growth for 1988.

9.2.1 Methods

The first growth calibration end point was the daily intake of food. Data on the stomach contents of Tule River trout sampled between 1986 and 1991 allowed us to estimate the wet weight of prey consumed per day, represented as a percentage of body weight (Table 9-2), which is an example of a simple, quantitative end point. To get these estimates, we converted trout length to weight using the Tule River length-weight relationship for each species. We estimated daily consumption (C, grams wet weight) as

$$C = 24\ E\ S\ , \qquad \text{(eq. 9-2)}$$

where S is the average stomach contents (g) over 24 hours, and E is the instantaneous gastric evacuation rate. The gastric evacuation rate was estimated for each trout as a function of the temperature (T) at the time the trout was collected. We used the Elliott and Persson (1978) relationship:

$$E = 0.05\ \exp(0.112\ T)\ . \qquad \text{(eq. 9-3)}$$

Table 9-2. **Summary of stomach contents data collected in the Tule River, California, and our estimates of daily consumption**

Adult Trout (N = 523)					
Variable	**Units**	**Mean**	**Std. Dev.**	**Minimum**	**Maximum**
Stomach Contents	mg	10.6	17.2	0.00	166.0
Daily Consumption	g	0.22	0.20	0.00	3.8
Daily Consumption	% body wt	0.78	0.60	0.00	10.0
Age 0 Trout (N = 32)					
Variable	**Units**	**Mean**	**Std. Dev.**	**Minimum**	**Maximum**
Stomach Contents	mg	2.8	2.1	0.06	8.7
Daily Consumption	g	0.08	0.03	0.00	0.24
Daily Consumption	% body wt	1.6	1.5	0.03	15.8

Because these field estimates of mean consumption as a percentage of body weight seemed on the low side (Brett 1979; Brett and Groves 1979), we adopted the observed range as a guideline. We considered a daily foraging intake of 0 to 15% of body weight to be reasonable, with values higher for Age 0 trout than older trout.

The second growth calibration end point involved the two prey availability parameters, m_{drift} and f_B . We required model trout to exhibit a mix of foraging modes, with some trout drift feeding and some benthic feeding; this is an example of a simple, qualitative end point. Studies of trout foraging behavior in streams suggest that trout generally use a mix of foraging modes (e.g., Jenkins 1969; Grant and Noakes 1987). A MathCad worksheet simplified the calibration by allowing us to generate reasonable initial guesses of prey availability parameters without the full complexity of the model. We shifted the benthic and drift intake curves (see Fig. 5-2) to encompass the range of daily intake observed in the Tule River.

The third growth calibration end point was growth itself. We were fortunate to have end-of-June and end-of-September estimates of trout sizes for the Tule River. These size estimates reflect the outcome of many events and the integration of many bioenergetic processes throughout the year and provided us with a complex, quantitative end point (Table 9-1). We calibrated annual growth by adjusting four parameters: (1) the availability factor for benthic prey, f_B ; (2) the slope between drift rate and velocity, m_{drift} ; (3) the factor scaling the availability of drift-feeding habitat, c_{stat} , which controls the amount of stream habitat suitable for drift foraging; and (4) the parameter f_{dem2} , which decreases the time spent foraging by larger trout under the assumption that larger trout have reduced weight-specific consumption requirements (Brett 1979). The third parameter was important in matching observed species differences because of the advantage that brown trout have in securing feeding stations in the model. The fourth parameter was important in matching growth for all ages of trout. Once the model was calibrated for 1988, we tested the model by using the same parameters for the second year, 1991.

9.2.2 Results and Discussion

The simulated length distributions are in excellent agreement with the observed distributions for water year 1988 (Fig. 9-3). When we used the 1988 parameter values for water year 1991, we also had excellent agreement of simulated and observed distributions (Fig. 9-4). These comparisons indicate that our coupling of an individual-based bioenergetics model with a simulation of stream habitat provides accurate estimates of trout growth, including a realistic amount of variation in length. Simulated length distributions showed considerable overlap with field distributions in all cases.

Fig. 9-3. Comparison of simulated and field-estimated length distributions by age class for (a) rainbow trout and (b) brown trout in fall 1988. Each distribution is characterized by the median (solid vertical line), mean (dotted vertical line), middle 50% (bar), 95% confidence interval (horizontal line), and minimum and maximum (open circles). The distributions for field-estimated lengths are based on data from Studley et al. (1995; Appendix M).

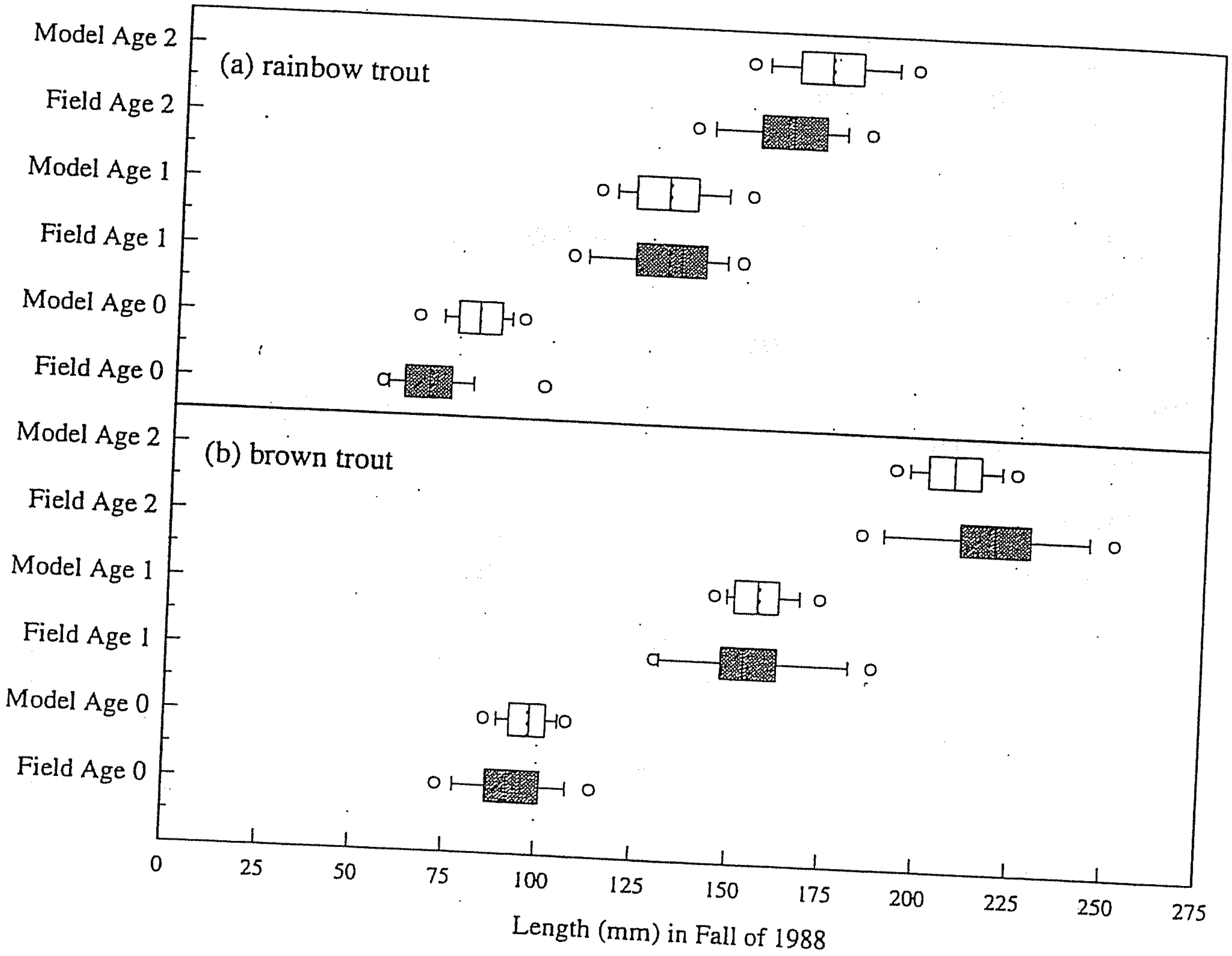
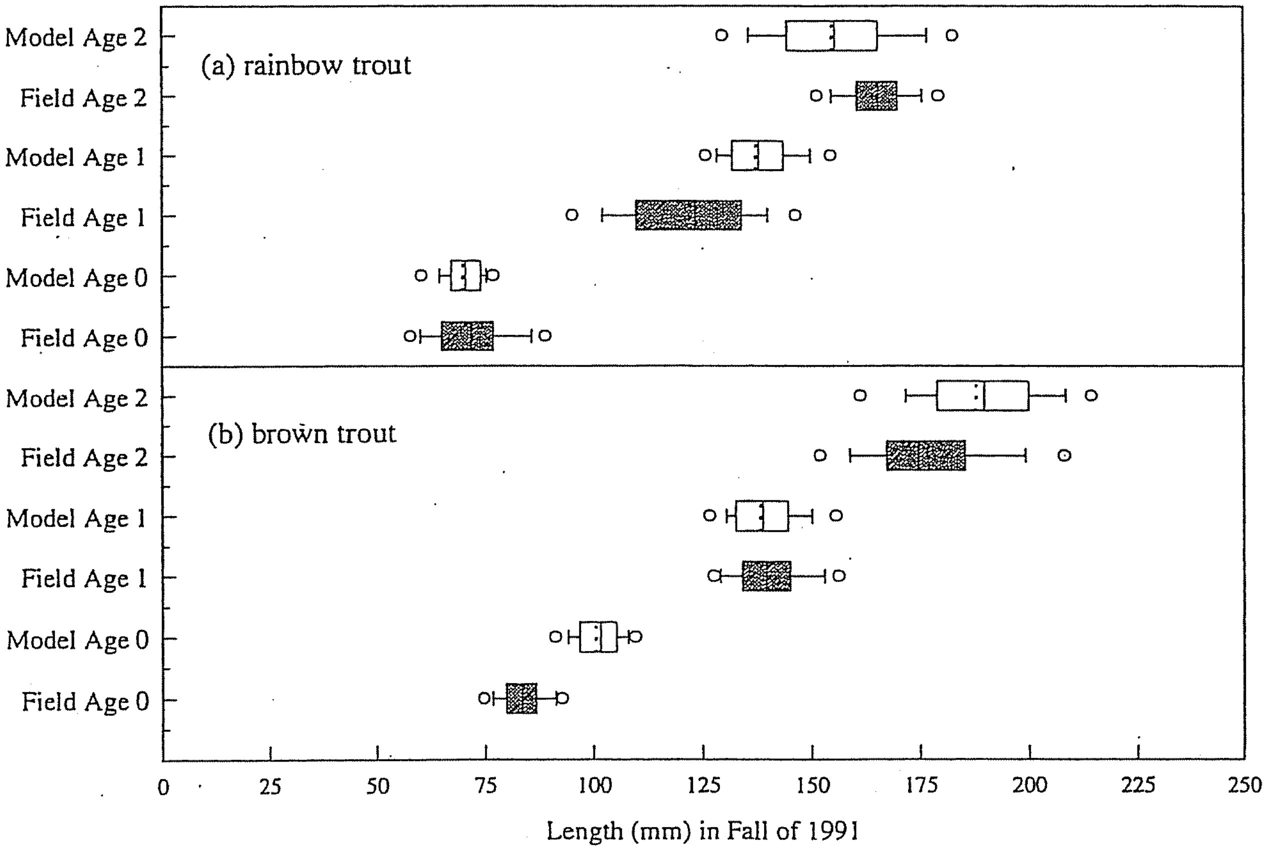


Fig. 9-4. Comparison of simulated and field-estimated length distributions by age class for (a) rainbow trout and (b) brown trout in fall 1991. Each distribution is characterized by the median (solid vertical line), mean (dotted vertical line), middle 50% (bar), 95% confidence interval (horizontal line), and minimum and maximum (open circles). The distributions for field-estimated lengths are based on data from Studley et al. (1995; Appendix M).



9.3 Calibration of Mortality Risks During Incubation

Mortality during incubation is caused by several factors, including dewatering and scouring of the redd, extreme temperatures, and superimposition (Sect. 8.1). No quantitative field information has been collected in the Tule River to provide an empirical check on our simulation of these four mortality factors. In addition, we represent other factors that cause mortality by a background mortality rate. We first adjusted the parameters for the four specific factors and then adjusted the background mortality to help match field abundances of Age 0 trout in the fall for water years 1988 and 1991.

9.3.1 *Methods*

A flood event on March 4, 1991, has been blamed for the low numbers of Age 0 brown trout in the fall 1991 population survey. It was believed that the daily average flow on that date would not have been sufficient to destroy the redds, but that the daily peak flow of 1200 cfs was sufficient. We used three parameters to calibrate scouring mortality. At extreme flows, we predict local velocities by assuming that all habitat units share a common average water surface slope and set the roughness parameter to a mimimum value, N_{min}. Two additional calibration parameters, P_{sc1} and P_{sc2}, relate the probability of redd scouring to velocity. We adjusted N_{min} , P_{sc1} , and P_{sc2} until more than 75% of simulated redds were destroyed at the 1200 cfs flow, but not at flows half that magnitude. Finally, we adjusted the background mortality rates (P_{bkgd}) so that the simulated fall abundances of Age 0 trout were in reasonable agreement with observed abundances. Although brown and rainbow trout have different background mortality rates, we constrained the rates to be the same for both water years.

Fig. 9-5. Comparison of simulated and field-estimated abundances by age class for (a) rainbow trout and (b) brown trout in fall 1988. Each distribution is characterized by the median (solid vertical line), mean (dotted vertical line), middle 50% (bar), 95% confidence interval (horizontal line), and minimum and maximum (open circles). The distributions for field-estimated abundances are calculated from density estimates (number/100 m of stream) (Studley et al. 1995; Appendix M).

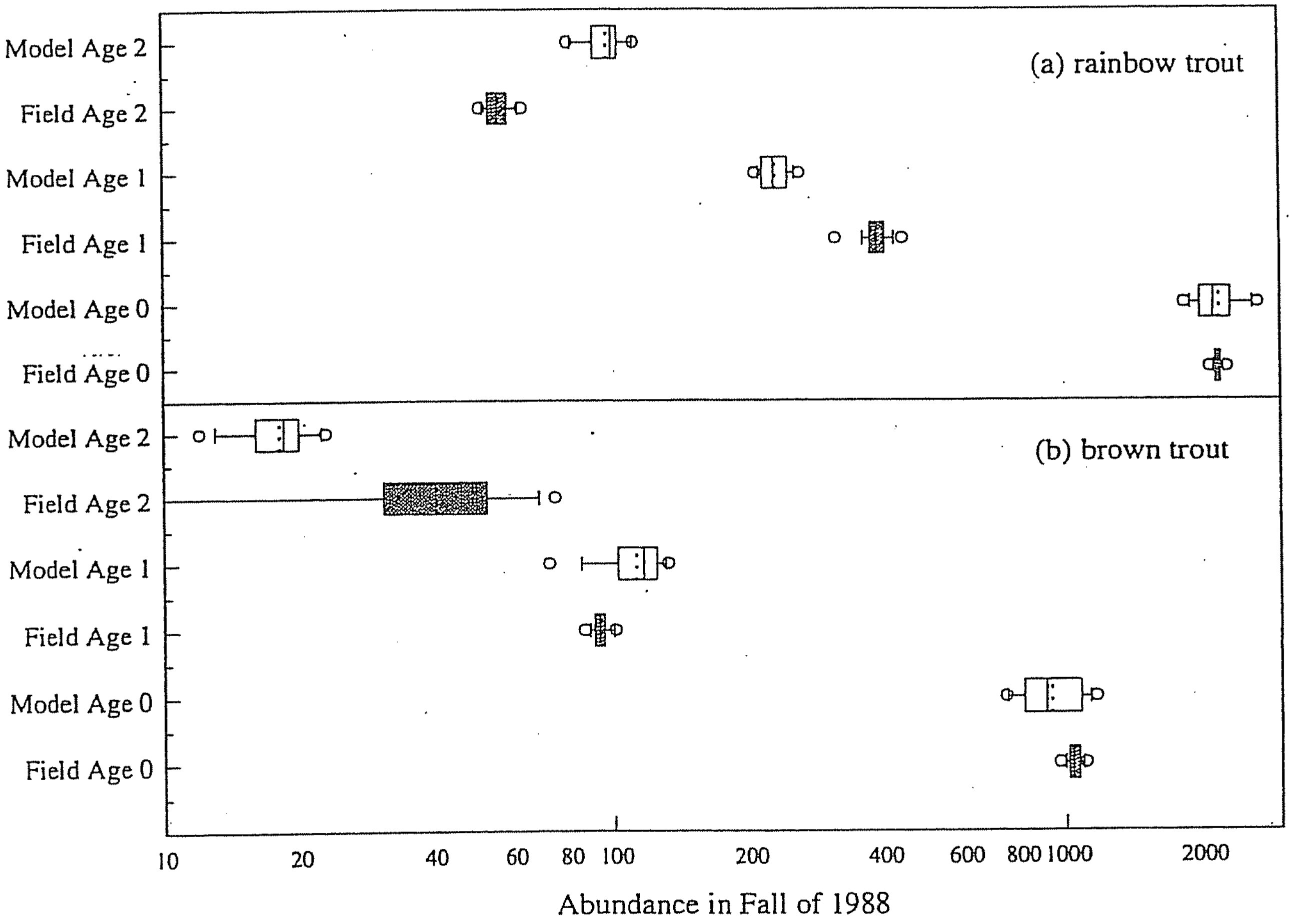
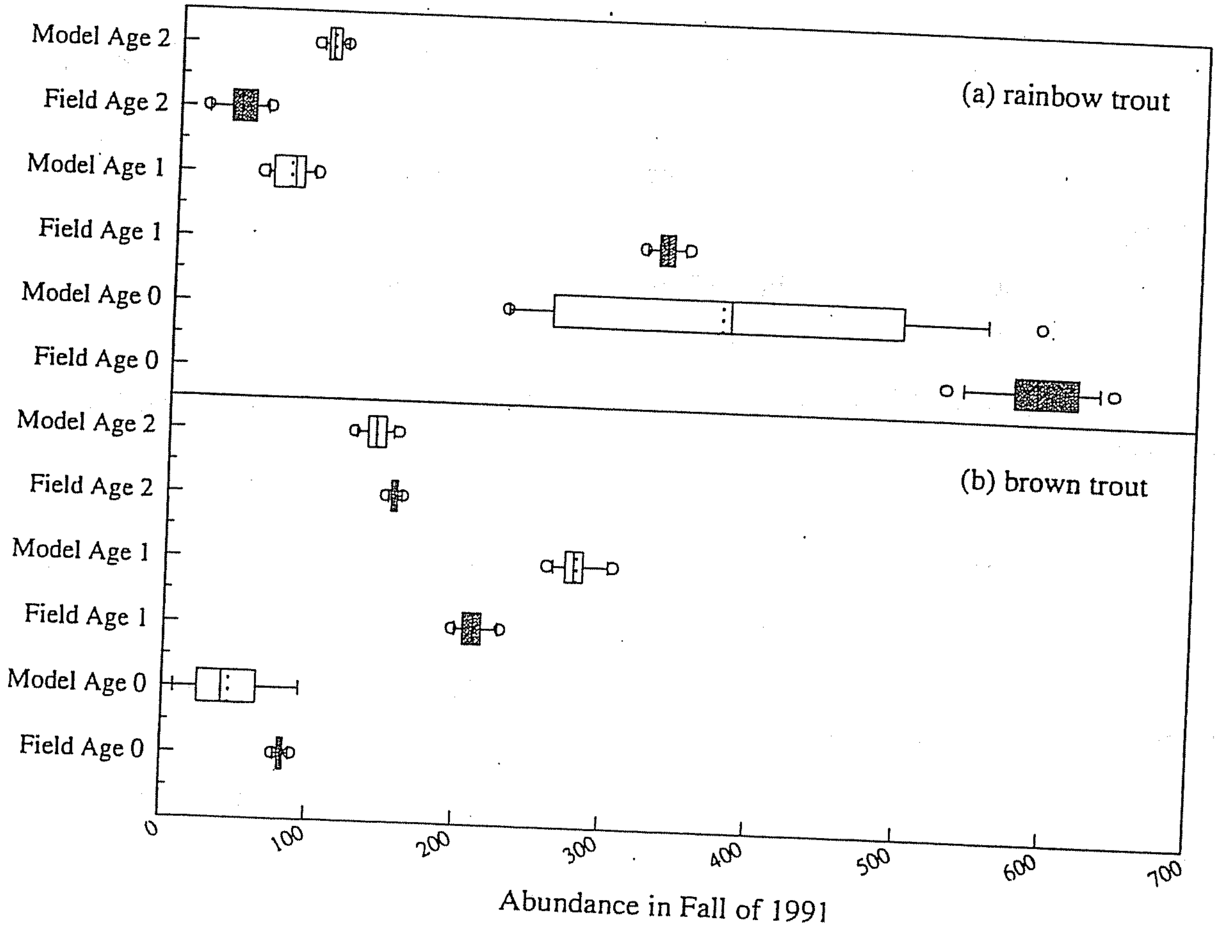


Fig. 9-6. Comparison of simulated and field-estimated abundances by age class for (a) rainbow trout and (b) brown trout in fall 1991. Each distribution is characterized by the median (solid vertical line), mean (dotted vertical line), middle 50% (bar), 95% confidence interval (horizontal line), and minimum and maximum (open circles). The distributions for field-estimated abundances are calculated from density estimates (number/100 m of stream) (Studley et al. 1995; Appendix M).



9.3.2 *Results and Discussion*

Age 0 abundances varied among the ten replicate simulations (Figs. 9-5 and 9-6), reflecting that mortality during incubation (and after emergence up until the time of the fall survey) is variable and unpredictable. Field and laboratory studies of spawning and incubation would likely provide an empirical basis for better simulating these mortality factors, thus reducing the uncertainity of our predictions of Age 0 recruitment.

For rainbow trout, the 2 water years offer a marked contrast in causes of mortality during the incubation period (Figs. 9-7 and 9-8). Low temperatures and high flows in 1991 delayed rainbow trout spawning nearly a month, compared to water year 1988. This delayed emergence from mid-June (1988) to mid-July (1991). Although they developed faster in 1991, rainbow trout eggs and alevins suffered high mortality from the high temperatures (>16°C) in July 1991. Dewatering occurred in both years, but the percentage of redds affected was higher in 1991 because redds were constructed during high flows that later decreased.

For brown trout, scouring on March 4, 1991, was the dominant factor in the model causing mortality during the incubation period. Flows from October to early December were low and stable in both years, so that mortality because of dewatering did not occur. Mortality due to temperature extremes did not occur in either year, because the temperature regime remained within the optimum range specified in the model. Some losses due to superimposition and background mortality did occur.

9.4 Calibration of Mortality Risks for Age 0 and Older Trout

Little is known, quantitatively, about the relative importance of the different mortality risks that reduce the abundance of brown and rainbow trout cohorts over time. We represented several mortality risks for Age 0 and older trout in the model (Sect. 8). Values for the parameters in these formulations are not well-grounded on empirical data, except for fishing. In addition, other risks exist that we have not mechanistically represented, such as predation and emigration from the stream segment.

Fig. 9-7. Percentage of the cumulative number of rainbow trout eggs and alevins dying as a function of date during the incubation period due to each of the five risks of mortality. This example shows one replicate simulation for 1987-88.

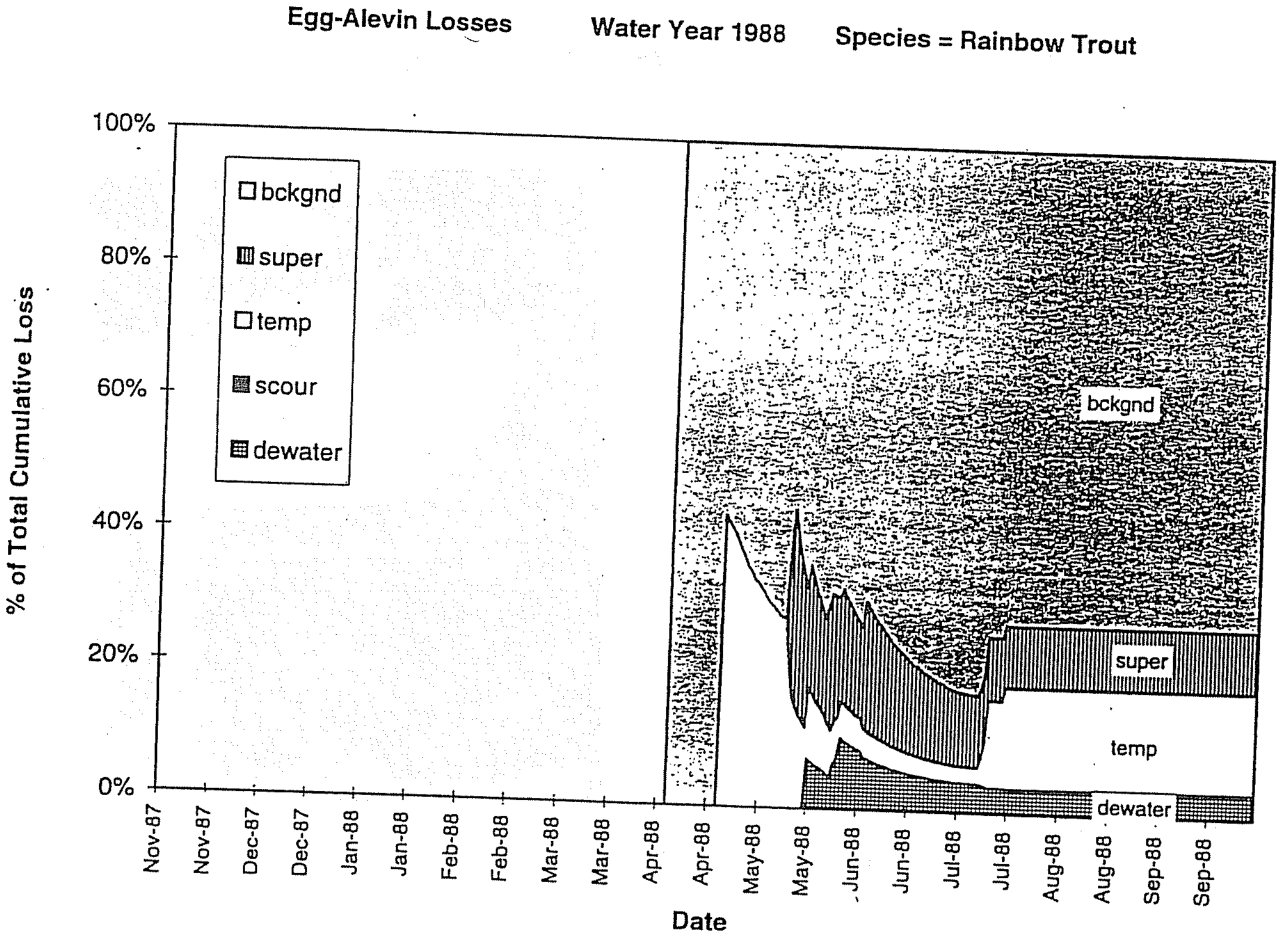
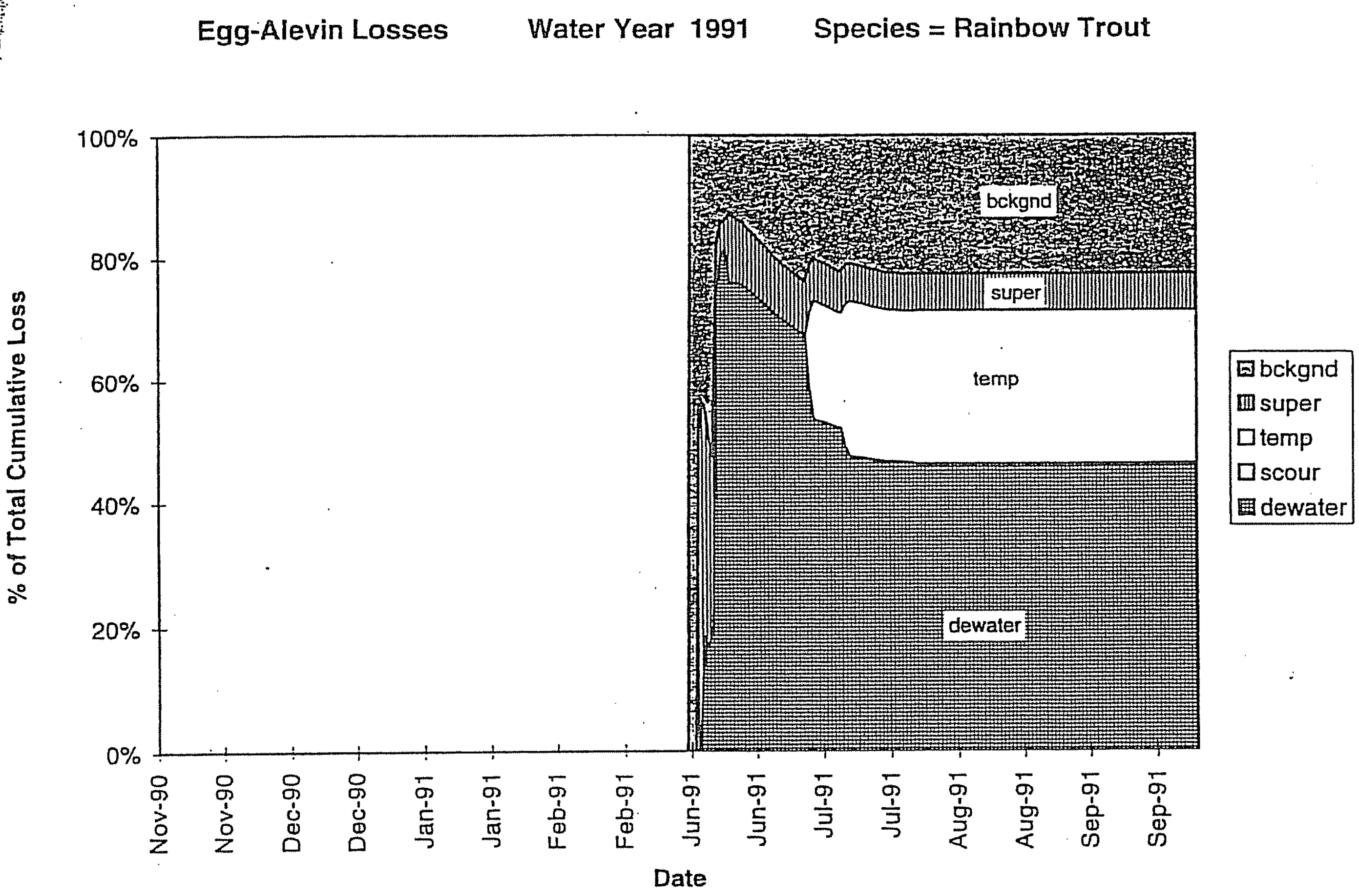


Fig. 9-8. Percentage of the cumulative number of rainbow trout eggs and alevins dying as a function of date during the incubation period due to each of the five risks of mortality. This example shows one replicate simulation for 1990 - 1991.



9.4.1 Methods

The parameters involved in the calibration were (1) F_{Lmax}, the minimum risk of natural mortality for a large trout in good condition (Fig. 8-1); (2) Z_{act}, the instantaneous rate of natural mortality for a trout while active; (3) P_{fmax}, the maximum daily risk of fishing mortality; and (4) P_{repro}, the risk of mortality following spawning. Because variability is high in model predictions of abundance, we simulated ten replicates for each year and report the distribution of ten abundance estimates.

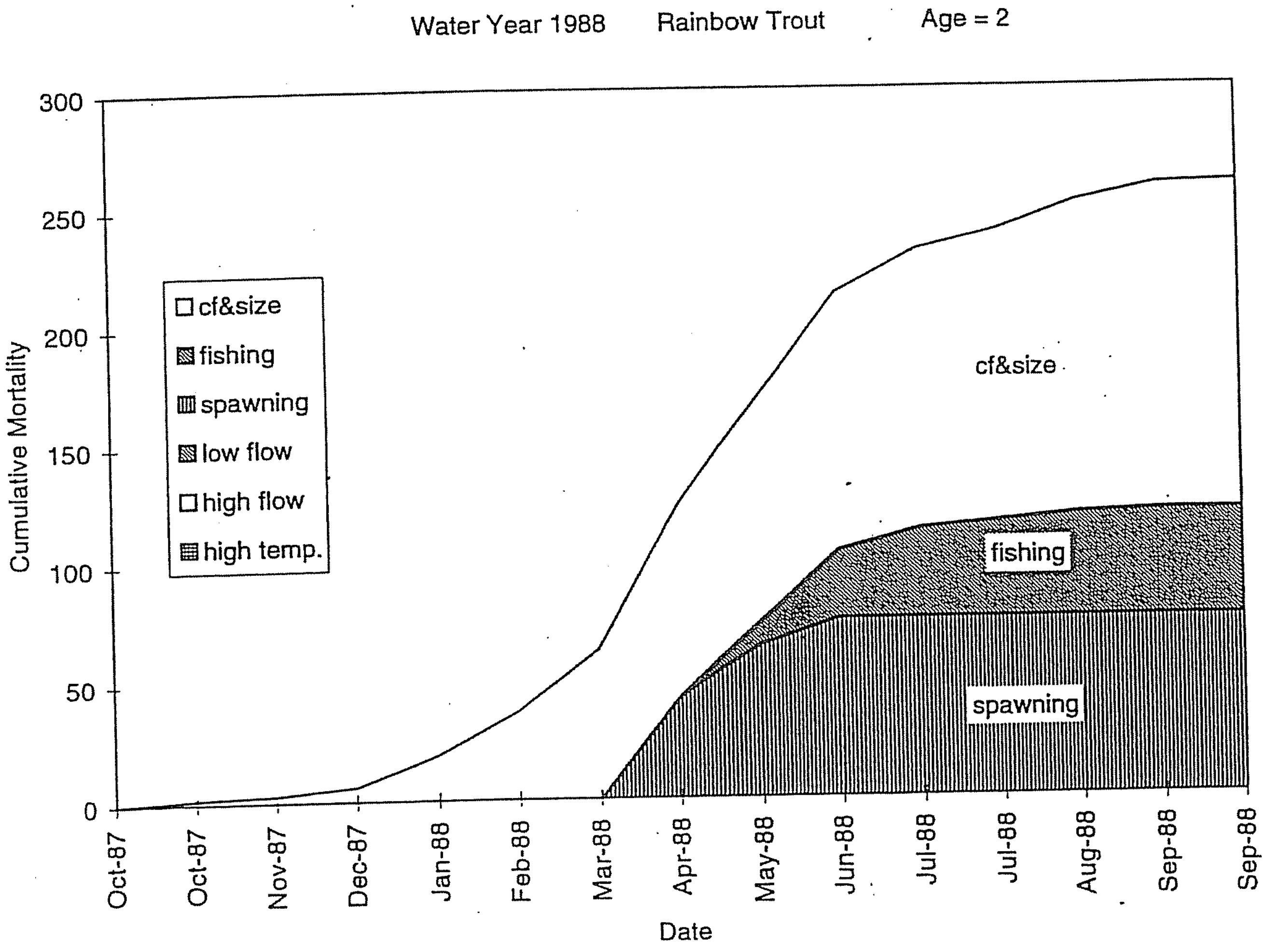
9.4.2 Results and Discussion

Fall abundances predicted after one year's simulation generally agreed with those observed in the field for each species and age class, especially Age 0, for water years 1988 and 1991 (Figs. 9-5 and 9-6). However, matching Age 1 and Age 2 abundances for both species and both years was difficult; four of the eight comparisons show no overlap in distributions (Figs. 9-5 and 9-6). This leaves us with precise, but not always accurate, predictions. During calibration, correcting one problem without creating others was difficult. Mortality due to high temperature, high velocity, and stranding occurred only rarely in the simulations (Fig. 9-9), as expected for this segment of the Tule River.

9.5 Calibration of Habitat Use

Habitat use is an indirect consequence of nearly every other process in the model. A few of the most important processes influencing habitat use are flow, size of a trout, profitability of foraging, avoidance of predation and other mortality risks, requirements of a suitable habitat, and exclusion by other trout. Parameters involved in the calibration of habitat use were (1) a_{Vmax} , b_{Vmax} , and V_{add} , which link maximum water column velocity to average water column velocity; and (2) d_{move}, the minimum depth (as a fraction of trout length) tolerated by model trout before moving.

Fig. 9-9. Cumulative number of Age 2 rainbow trout dying as a function of date due to each of the six risks of mortality. This example shows one replicate simulation for 1987 - 1988.



9.5.1 Methods

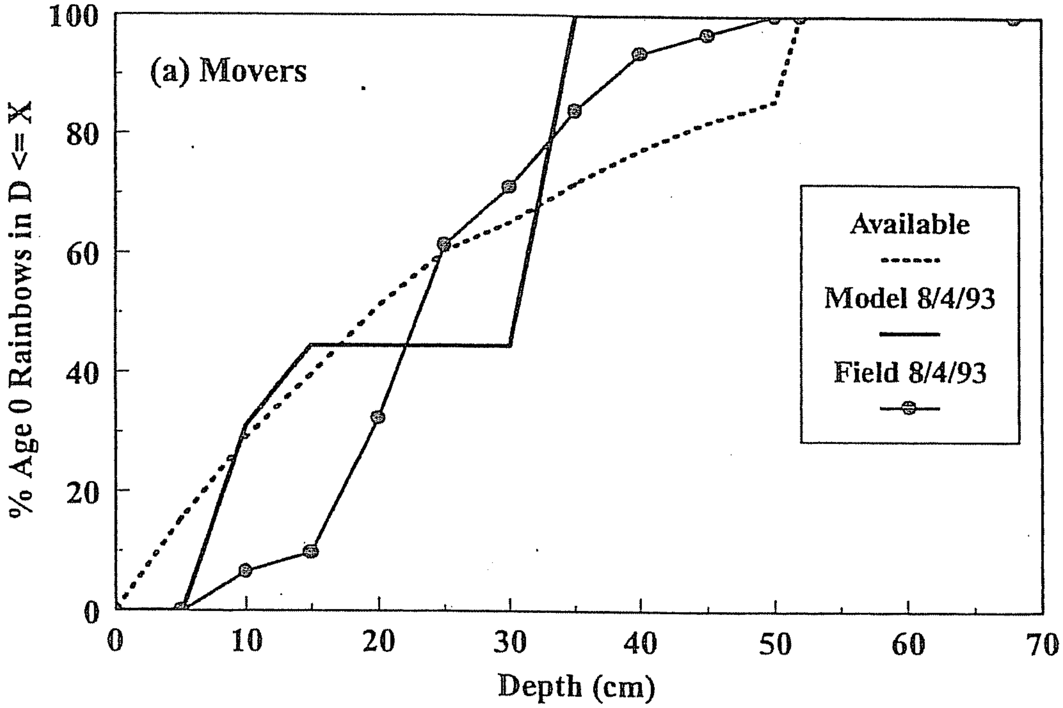
Wise and Lifton (1994) collected habitat use information for rainbow trout of all ages and for Age 0 brown trout in the Tule River during two trips (August 3–5 and September 16–18, 1993). We focused our calibration on Age 0 rainbow trout because of the large sample size. These data provided quantitative field observations on the use of depth, focal velocity, and mean column velocity. We used the model to simulate trout habitat use for water year 1993 and compared simulated habitat use by Age 0 rainbow trout on August 4, 1993, with that observed during the field study on August 3–5, 1993.

One purpose of the comparison was to evaluate the differences in habitat use by movers and stayers (Grant and Noakes 1987). The observations of trout behavior in the field allowed us to classify each trout as a drift forager (stayer) or benthic forager (mover). Most of the drift foragers were observed in the middle of the water column, but some were feeding at the surface. Most of the benthic foragers were resting rather than feeding, making the comparison with movers less than ideal.

9.5.2 Results and Discussion

The model did a reasonable job of predicting the depths (Fig. 9-10) and focal velocities (Fig. 9-11) used by Age 0 rainbow trout. More than 50% of the movers in the field were observed at zero focal velocity (Fig. 9-11a), although they commonly appeared to be resting rather than feeding on benthos; the model predicts less than 20%. As expected, drift foragers in the field and the model tended to use higher focal velocities than benthic foragers (Fig. 9-11), but the difference is less than might be expected. Optimal drift-feeding velocities were occupied by stayers, but not movers (see Fig. 5-2). This suggests that benthic feeders may be excluded from intermediate velocities by drift feeders holding feeding stations. The mean column velocities used by model drift feeders were somewhat higher and by benthic feeders were somewhat lower than those observed in the field (Fig. 9-12).

Fig. 9-10. Comparison of available depths and simulated and observed depths used by age 0 rainbow trout for (a) movers and (b) stayers. The Y-axes are cumulative percentage of Age 0 rainbow trout using depths (D) less than or equal to the depth coordinate on the X-axis.



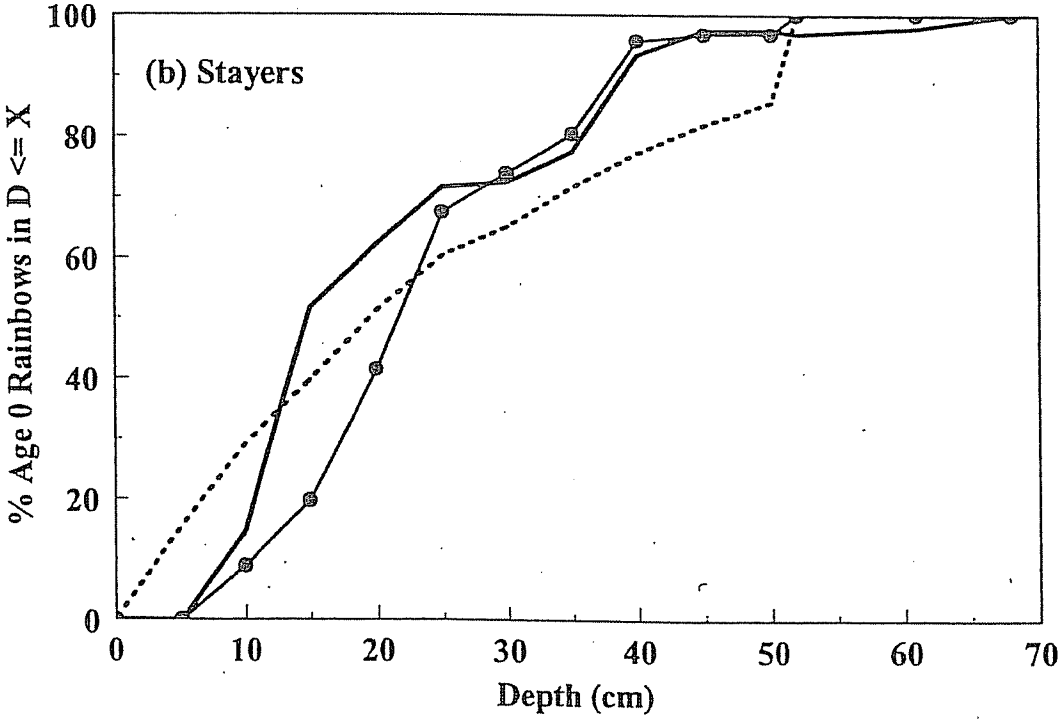
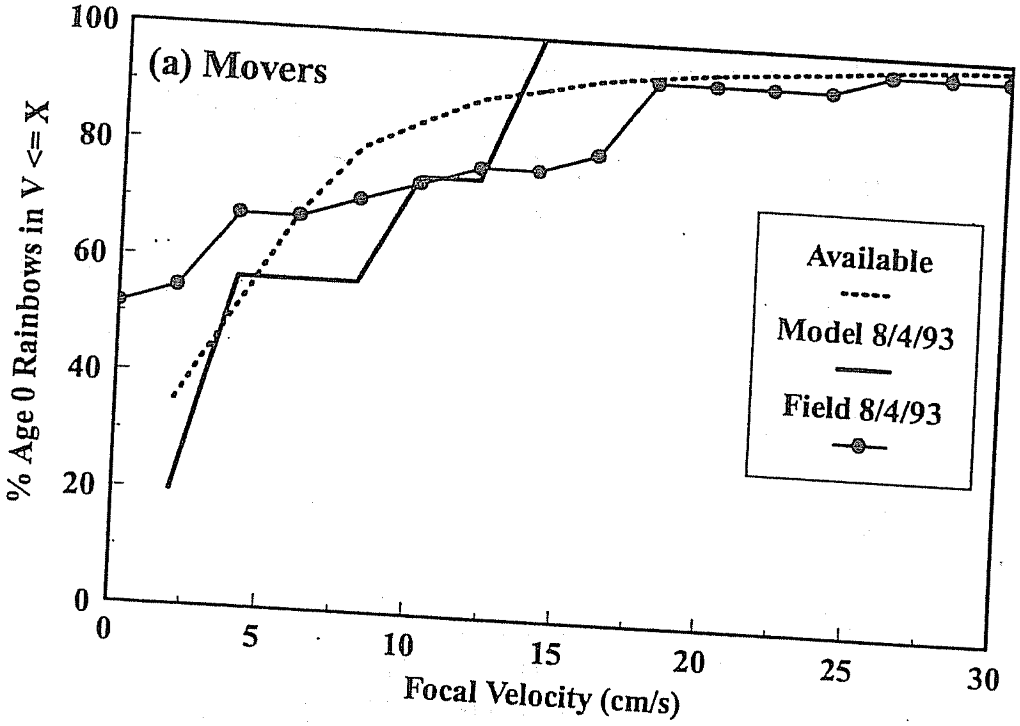


Fig. 9-11. Comparison of available mean focal velocities and simulated and observed mean focal velocities used by age 0 rainbow trout for (a) movers and (b) stayers. The Y-axes are cumulative percentage of Age 0 rainbow trout using mean column velocities (V) less than or equal to the velocity coordinate on the X-axis.



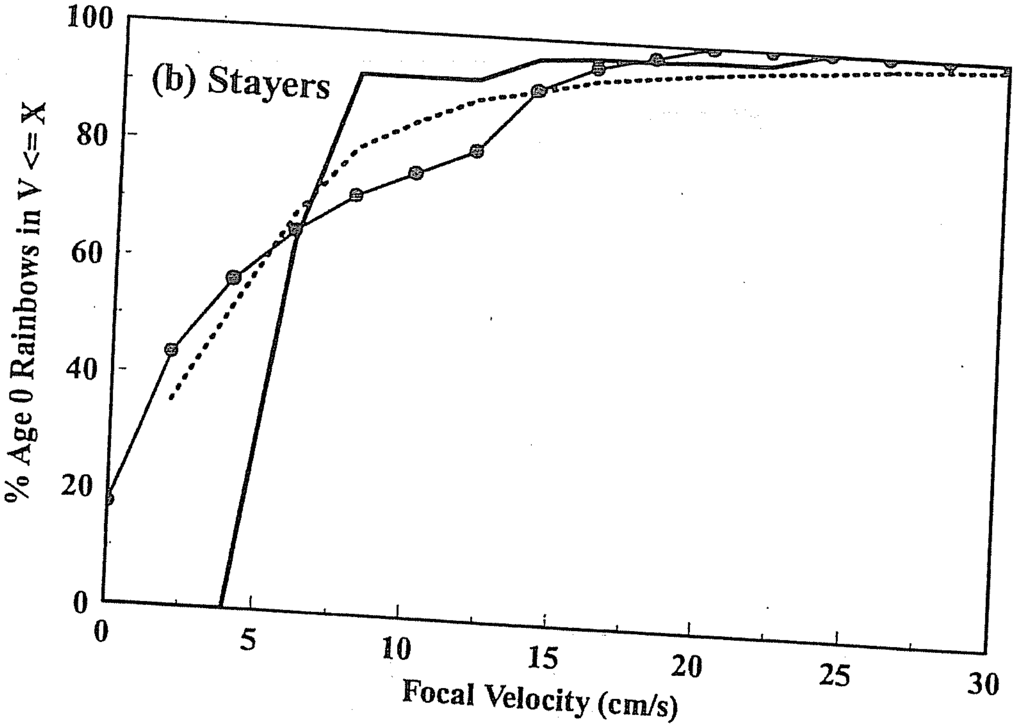
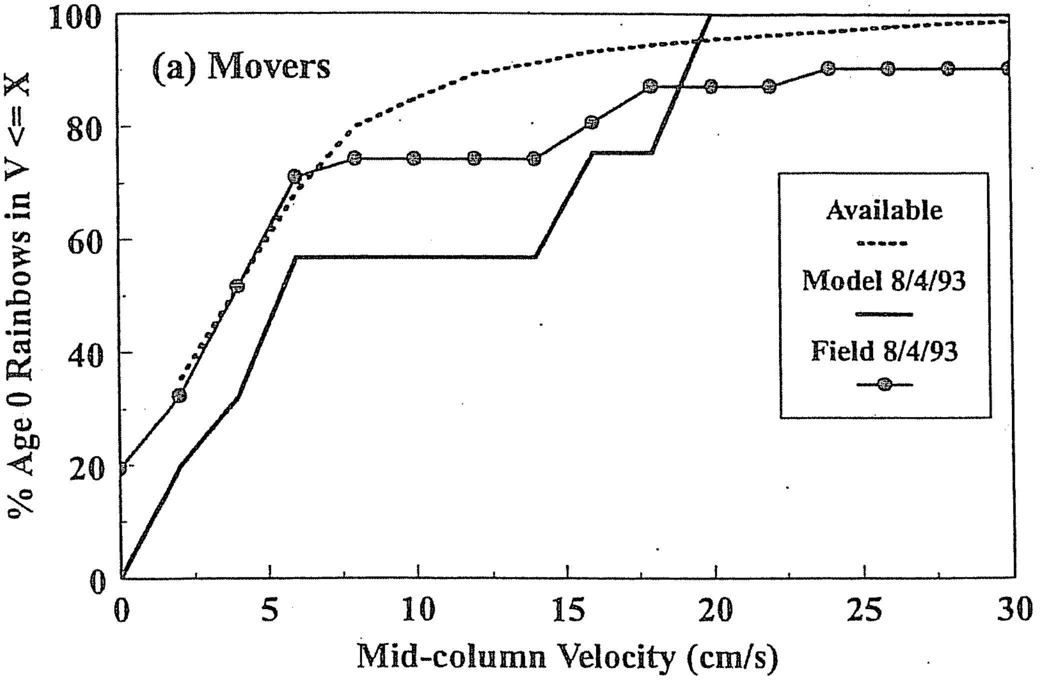
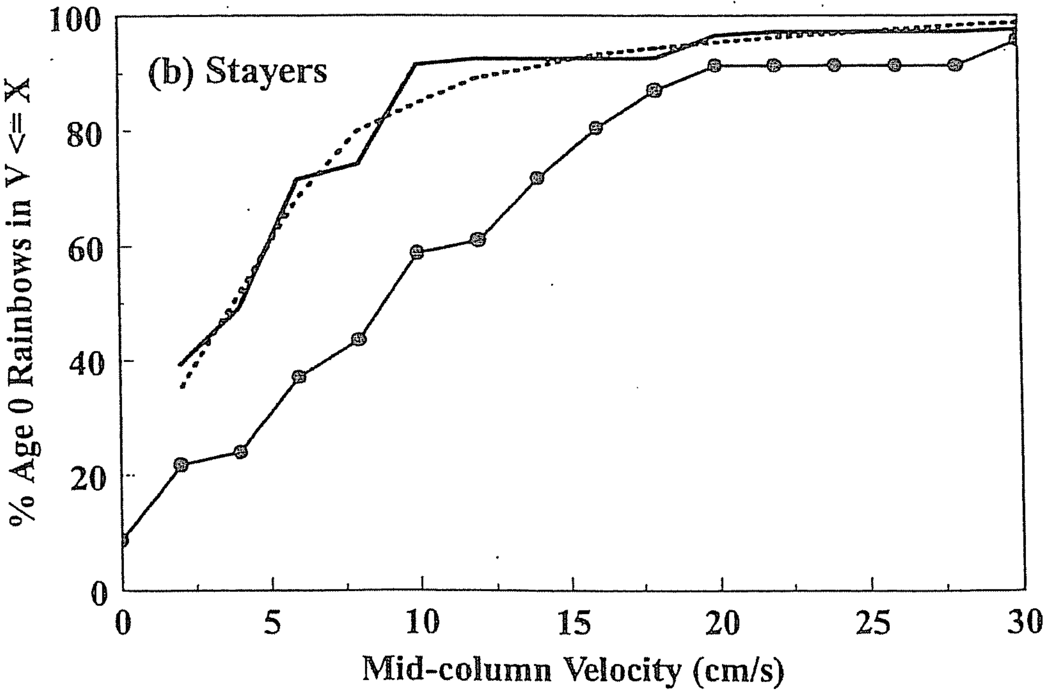


Fig. 9-12. Comparison of available mean column velocities and simulated and observed mean column velocities used by age 0 rainbow trout for (a) movers and (b) stayers. The Y-axes are cumulative percentage of Age 0 rainbow trout using focal velocities (V) less than or equal to the velocity coordinate on the X-axis.



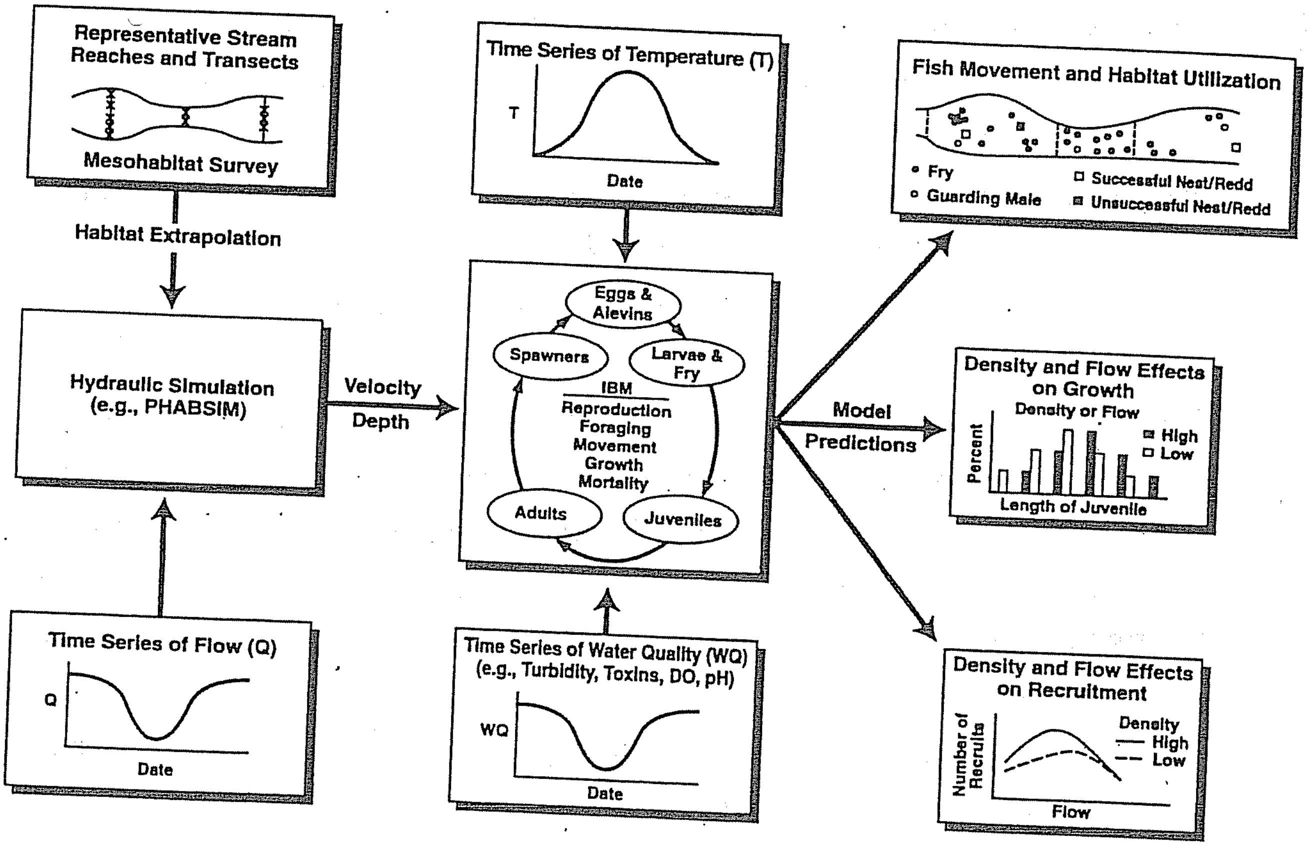


SECTION 10 DISCUSSION

This report describes an individual-based model for sympatric populations of brown and rainbow trout in a stream habitat. Hatchery rainbow trout are included as a third species. The model provides a tool for predicting flow effects on trout populations by linking the hydraulic component of the Physical Habitat Simulation (PHABSIM) methodology to an individual-based population modeling approach (Fig. 10-1). PHABSIM simulates the spatial distribution of depth and velocity at different flows. The individual-based model simulates the reproduction, foraging, consumption, energetic costs, growth, habitat utilization, movement, and mortality of individual fish, and enables population attributes to be determined from relevant attributes of individual fish. The spatially explicit nature of the model permits evaluation of behavioral responses that are used by fish to cope with temporary setbacks in habitat quality. This linked mechanistic modeling approach readily lends itself to the iterative process of making predictions, testing against field data, improving the model, and making more predictions.

The model has been applied to a stream segment in the Tule River, California. Physical and biological data from this site were used as input to the model. The model was calibrated for water years 1988 and 1991. Given initial model populations on October 1, parameters were adjusted until model predictions of length and population abundance (including production of a new year class) on June 30 and September 30 of the following year were in reasonable agreement with observed estimates. In calibrating the model, we also focused on comparing the predicted and observed patterns of habitat utilization at the mesohabitat level (i.e., pools, pocket waters, riffles) and the microhabitat level (i.e., depths, velocities). Given the apparent importance of extreme events, flood events in particular, we assured that the model was able to simulate the results of the March 4, 1991, flood in scouring brown trout redds and greatly reducing the strength of that incoming year class.

Fig. 10-1. Schematic of the model for sympatric populations of brown and rainbow trout illustrating links between (a) characterization of the physical habitat and (b) an individual-based model representing the different life stages and processes underlying reproduction, growth, and mortality. The model is a tool for evaluating the effects of alternative flow and temperature regimes based on measurable responses such as habitat use, growth, abundance, and recruitment.



In this section we discuss the tradeoff between increasing realism and complexity and research needs.

10.1 Tradeoff between Realism and Complexity

Population models tend to be evaluated primarily by their ability to simulate numbers or density of individuals. However, calibrating a model to match observations of abundance within a single year is relatively easy. In the case of this trout model, the absence of data on how many trout die, when they die, and from what cause means that considerable uncertainty exists in the parameters used to characterize mortality. Thus, a fortunate (but unfortunate) degree of freedom is available to adjust these parameters within acceptable bounds to achieve most, but not all (e.g., Fig. 9-6, Age 1 rainbow trout), observed results.

This freedom is not the case in calibrating the model to simulate observations of length or habitat utilization. Simulated length-frequency distributions and habitat utilization reflect our entire bioenergetics formulation involving foraging, movement, and respiration. These formulations, in turn, are dependent on our representation of the physical habitat involving PHABSIM and the mapping of depths, widths, and velocities from donor to receptor habitat units and cells as a function of flow. The parameters involved in most of these formulations are more strongly based on actual measurements than is the case for mortality. Consequently, we view our success in calibrating the model to match observed lengths and habitat utilization as a more rigorous test of the model than matching abundances.

The primary reason for developing this model has been to link PHABSIM techniques for characterizing physical habitat with an individual-based population model to provide a new tool for evaluating the effects of alternative flow and temperature regimes on trout populations (Fig.10-1). The ongoing Pacific Gas & Electric Company Altered Flows Project and other studies have documented that factors other than those involved in a PHABSIM analysis of weighted useable area can limit trout populations. The individual-based population model is used in place of habitat suitability indices. This substitution increases realism by mechanistically representing the processes underlying the reproduction, growth, and survival of individuals as they pass through their life cycle.

As with all modeling, however, the price of an increase in realism is an increase in complexity (Ney 1993). The model is now at a stage of development where evaluation of this tradeoff between realism and complexity is needed. Instream-flow assessments at what might be termed the scoping level are at one extreme. Application of this tool is not appropriate in these cases because of increased costs and time required (1) to obtain the necessary site-specific data beyond that needed for a PHABSIM analysis, (2) to reconfigure the model to that site, (3) to perform the model runs, and (4) to interpret the results. In-depth studies such as the PG&E Altered Flows Project (Studley et al. 1995) are at the other extreme. This model is an ideal tool in these cases for the iterative cycle of designing studies, carrying them out, interpreting the results, and making predictions. Between these two extremes are assessments that pit water for fish against water for other uses and which have a great deal of money at stake compared to the money needed to apply this model.

Demonstration assessments that use this modeling approach to develop cost-effective flow releases are now needed. These demonstrations will likely require reconfiguring the model to site-specific conditions such as a longitudinal temperature gradient, thermal refuges associated with deep pools and groundwater inflow, tributary streams, and other fish species. These demonstrations may also involve simplifying the model to better address the assessment questions being posed in combination with the data available.

10.2 Research Needs

Developing a model of the type described in this report involves integration and synthesis of information, which for brown and rainbow trout was considerable. Nonetheless, several of our process formulations and parameter estimates are limited by a lack of information. This will always be the case. The thirst for site-specific data for all processes represented in the model and for yet one more year of field data on growth, abundance, and habitat utilization under different environmental conditions is unquenchable.

On the basis of our experience with this model, we have developed a list of research needs that we identify as high priority. The recommended studies could be performed at reasonable cost and effort and would be helpful in reducing uncertainty in model predictions and in increasing the predictability of the effects of alternative flow and temperature regimes on trout populations. Although we have focused on one study segment in one stream in our baseline simulations, we consider the research needs listed below as relevant for all Sierra Nevada trout streams.

The research needs are listed using the section headings from this report. **Our criterion for identifying a research need is that better information has the potential of substantially changing model predictions (and their interpretation).**

Physical Habitat (Sect. 2)

1. Perform a mesohabitat survey not only at base flow but at a substantially higher flow. Estimate water slope for each habitat unit at both flows. Develop a predictive approach for how mesohabitat types and sizes change with flow.

2. Develop a new methodology (perhaps statistical) to characterize the physical habitat of a stream from the point of view of how that habitat is used on a daily *average* basis by the different life stages of trout as reflected in the integrative response variables of reproduction, growth, and survival. Compare this new methodology with the PHABSIM methodology.

Spawning (Sect. 3)

1. Compare the characteristics of trout that are old enough and large enough to spawn, but that do not spawn, with the characteristics of trout that do spawn.

2. Estimate the variability among populations of rainbow and brown trout in Sierra Nevada streams in the two parameters that relate fecundity to trout length (eq. 3-2).

Development and Mortality in the Redd (Sect. 4)

1. Develop and test a method to predict scouring mortality as a function of substrate composition, flow, depth, and average water column velocity.

2. Estimate the variability among populations of rainbow and brown trout in Sierra Nevada streams in the four temperature parameters relating daily probability of mortality of eggs and alevins caused by low and high temperatures (eq. 4-4).

3. Evaluate the factors associated with superimposition for trout in Sierra Nevada streams at low versus high densities of trout.

4. Compare the success of rainbow trout redds, in terms of emergence of fry, for early versus late spawners.

Growth: Foraging and Consumption (Sect. 5)

1. Estimate the temperature-dependent parameters of the equation for maximum consumption (eq. 5-14) for Age 0 (30–100 mm in length) rainbow and brown trout.

2. Extend the experiments of Hill (1989) on reactive distance and probability of prey capture to a wider range of temperatures, light conditions, and sizes of trout.

Growth: Energetic Costs (Sect. 6)

1. Estimate the temperature-dependent parameter in the equation for standard respiration (eq. 6-5) for Age 0 (30–100 mm in length) rainbow and brown trout.

Habitat Utilization and Movement (Sect. 7)

1. See Item 2 under Physical Habitat.

2. Evaluate our formulation for characterizing access to instream cover (Sect. 7-2) through field and laboratory experiments.

3. Evaluate the assumption that downstream emigration out of a study segment is approximately balanced by downstream immigration into a study segment.

Mortality (Sect. 8)

1. Evaluate existing data on trout density, angler effort, and catch for trout populations in Sierra Nevada streams to estimate the extent to which the sport fishery operates in a density-dependent (i.e., compensatory) manner.

2. Evaluate the extent to which stocking of hatchery rainbow trout alters the foraging, growth, habitat utilization, movement, and mortality of other trout.

3. Determine the pattern of downstream movement of rainbow and brown trout in Sierra Nevada streams as a function of flow, season, size of trout, and density of trout. Test the paradigm which states that an important density-dependent mechanism is that "excess" fry are unable to establish territories and passively move downstream into oblivion.

SECTION 11 BIBLIOGRAPHY

Alexander, G. R. 1977. Consumption of small trout by large predatory brown trout in the North Branch of the Au Sable River, Michigan. Fisheries Research Report No. 1855, Michigan Department of Natural Resources, Ann Arbor, MI.

Allan, I. R. H., and J. A. Ritter. 1977. Salmonid terminology. Journal du Conseil pour Internationale Exploration du Mer 37:293-299.

Anderson, D. W. 1983. Factors affecting brown trout reproduction in southeastern Minnesota streams. Minnesota Department of Natural Resources, Division of Fish and Wildlife, Investigational Report 376, Minneapolis, MN.

Angradi, T. R., and J. S. Griffith. 1990. Diel feeding chronology and diet selection of rainbow trout (Oncorhynchus mykiss) in the Henry's Fork of the Snake River, Idaho. Canadian Journal of Fisheries and Aquatic Sciences 47:199-209.

Armour, C. L., and J. G. Taylor. 1991. Evaluation of the instream flow incremental methodology by U. S. Fish and Wildlife Service field users. Fisheries 16(5):36-43.

Avery, E. L. 1980. Factors influencing reproduction of brown trout above and below a flood water detention dam on Trout Creek, Wisconsin. Research Report 106. Wisconsin Department of Natural Resources, Madison, WI.

Avery, E. L. 1985. Sexual maturity and fecundity of brown trout in Central and Northern Wisconsin streams. Technical Bulletin No. 154. Wisconsin Department of Natural Resources, Madison, WI.

Bachman, R. A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Transactions of the American Fisheries Society 113:1-36.

Bagenal, T. B. 1969. Relationship between egg size and fry survival in brown trout Salmo trutta L. Journal of Fish Biology 1:349-353.

Bannon, E., and N. H. Ringler. 1986. Optimal prey size for stream resident brown trout (Salmo trutta): Tests of predictive models. Canadian Journal of Zoology 64:704-713.

Barrett, J. C., G. D. Grossman, and J. Rosenfield. 1992. Turbidity-induced changes in reactive distance of rainbow trout. Transactions of the American Fisheries Society 121:437-443.

Bart, J. 1995. Acceptance criteria for using individual-based models to make management decisions. Ecological Applications 5(2):411-420.

Beard, T. D., Jr., and R. F. Carline. 1991. Influence of spawning and other stream habitat features on spatial variability of wild brown trout. Transactions of the American Fisheries Society 120:711-722.

Bernstein, C., A. Kacelnik, and J. R. Krebs. 1988. Individual decisions and the distribution of predators in a patch environment. Journal of Animal Ecology 57:1007-1026.

Bernstein, C., A. Kacelnik, and J. R. Krebs. 1991. Individual decisions and the distribution of predators in a patch environment. II. The influence of travel costs and structure of the environment. Journal of Animal Ecology 60:205-225.

Bidgood, B. F., and A. H. Berst. 1960. Lethal temperatures for Great Lakes rainbow trout. Journal of the Fisheries Research Board of Canada 26:456-459.

Billard, R. 1992. Reproduction in rainbow trout: sex differentiation, dynamics of gametogenesis, biology and preservation of gametes. Aquaculture 100:263-298.

Bisson, P. A. 1978. Diel food selection by two sizes of rainbow trout (Salmo gairdneri) in an experimental stream. Journal of the Fisheries Research Board of Canada 35:971-975.

Bisson, P. A, J. L. Nielsen, R. A. Palmason, and L. E. Grove. 1982. A system of naming habitat in small streams, with examples of habitat utilization by salmonids during low stream flow. pp. 62-74. IN N. B. Armantrout, editor. Acquisition and Utilization of Aquatic Habitat Inventory Information. American Fisheries Society Western Division, Bethesda, MD.

Boisclair, D., and W. C. Leggett. 1989. The importance of activity in bioenergetics models applied to actively foraging fishes. Canadian Journal of Fisheries and Aquatic Sciences 46:1859-1967.

Brett, J. R. 1979. Environmental factors and growth. pp. 599-675. IN W. S. Hoar, D. J. Randall, and J. R. Brett, editors. Fish Physiology, Volume VIII, Bioenergetics and Growth. Academic Press, New York.

Brett, J. R., and N. R. Glass. 1973. Metabolic rates and critical swimming speeds of sockeye salmon (Oncorhynchus nerka) in relation to size and temperature. Journal of the Fisheries Research Board of Canada 30:379-387.

Brett, J. R., and T. D. D. Groves. 1979. Physiological energetics. pp. 280-352. IN W. S. Hoar, D. J. Randall, and J. R. Brett, editors. Fish Physiology, Volume VIII, Bioenergetics and Growth. Academic Press, New York.

Brock, T. D. 1981. Calculating solar radiation for ecological studies. Ecological Modelling 14:1-19.

Bromage, N., and R. Cumaranatunga. 1988. Egg production in the rainbow trout. pp. 63-138. IN F. Muir and J. Roberts, editors. Recent Advances in Aquaculture. Croom Helm, London.

Bromage, N., P. Hardiman, J. Jones, J. Springate, and V. Bye. 1990. Fecundity, egg size and total egg volume differences in 12 stocks of rainbow trout, Oncorhynchus mykiss Richardson. Aquaculture and Fisheries Management 21:269-284.

Campbell, R. F., and J. H. Neuner. 1985. Seasonal and diurnal shifts in habitat utilized by resident rainbow trout in western Washington Cascade mountain streams. pp. 39-48. IN F. W. Olson, R. G. White, and R. H. Hamre, editors. Symposium on Small Hydropower and Fisheries. American Fisheries Society, Western Division and Bioengineering Section, Bethesda, MD.

Carlander, K. D. 1969. Handbook of Freshwater Fishery Biology. Volume One. Iowa State University Press, Ames, IA.

Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology 9:129-136.

Coutant, C. C. 1970. Thermal resistance of adult coho (Onchorhynchus kisutch) and jack chinook (O. tshawytscha) salmon and adult steelhead trout (Salmo gairdneri) from the Columbia River. AEC Research and Development Report, BNWL-1508, Battelle Northwest, Richland, Washington.

Crisp, D. T., P. A. Carling. 1989. Observations on siting, dimensions and structure of salmonid redds. Journal of Fish Biology 34:119-134.

Cunjak, R. A. 1988. Physiological consequences of overwintering in streams: The cost of acclimitization? Canadian Journal of Fisheries and Aquatic Sciences 45:443-452.

Cunjak, R. A., and G. Power. 1987. The feeding and energetics of stream-resident trout in winter. Journal of Fish Biology 31:493-511.

Curry, R. A., J. Gehrels, D. L. G. Noakes, and R. Swainson. 1994. Effects of river flow fluctuations on groundwater discharge through brook trout, Salvelinus fontinalis, spawning and incubation habitats. Hydrobiologia 277:121-134.

Dickson, I. W., and R. H. Kramer. 1971. Factors influencing scope for activity and active and standard metabolism of rainbow trout (Salmo gairdneri). Journal of the Fisheries Research Board of Canada 28:587-596.

EA Engineering, Science, and Technology. 1994. Evaluation of factors causing variability in habitat suitability criteria for Sierra Nevada trout. Report 009.4-94.5. Pacific Gas and Electric Company, Department of Research and Development, San Ramon, CA.

Elliott, J. M. 1975a. Weight of food and time required to satiate brown trout, Salmo trutta L. Freshwater Biology 5:51-64.

Elliott, J. M. 1975b. Number of meals in a day, maximum weight of food consumed in a day and maximum rate of feeding for brown trout, Salmo trutta L. Freshwater Biology 5:287-303.

Elliott, J. M. 1975c. The growth rate of brown trout (Salmo trutta L.) fed on maximum rations. Journal of Animal Ecology 44:805-821.

Elliott, J. M. 1975d. The growth rate of brown trout (Salmo trutta L.) fed on reduced rations. Journal of Animal Ecology 44:823-842.

Elliott, J. M. 1976a. The downstream drifting of eggs of brown trout, Salmo trutta L. Journal of Fish Biology 9:45-50.

Elliott, J. M. 1976b. The energetics of feeding, metabolism and growth of brown trout (Salmo trutta L.) in relation to body weight, water temperature and ration size. Journal of Animal Ecology 45:923-948.

Elliott, J. M. 1976c. Energy losses in the waste products of brown trout (Salmo trutta L.). Journal of Animal Ecology 45:561-580.

Elliott, J. M. 1984a. Numerical changes and population regulation in young migratory trout Salmo trutta in a lake district stream, 1966–83. Journal of Animal Ecology 53:327-350.

Elliott, J. M. 1984b. Growth, size, biomass and production of young migratory trout Salmo trutta in a lake district stream, 1966–83. Journal of Animal Ecology 53:979-994.

Elliott, J. M. 1994. Quantitative Ecology and the Brown Trout. Oxford University Press, New York, NY.

Elliott, J.M., and L. Persson. 1978. The estimation of daily rates of food consumption for fish. Journal of Animal Ecology 47: 977-991.

Embody, G. C. 1934. Relation of temperature to the incubation periods of eggs of four species of trout. Transactions of the American Fisheries Society 64:281-292.

Fausch, K. D. 1984. Profitable stream positions for salmonids: Relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441-451.

From, J., and G. Rasmussen. 1984. A growth model, gastric evacuation, and body composition in rainbow trout, Salmo gairdneri Richardson, 1836. Dana 3:61-139.

Fry, F. E. J. 1971. The effect of environmental factors on the physiology of fish. pp. 1-63. IN W. S. Hoar and D. J. Randall, editors. Fish Physiology, Volume VI. Academic Press, New York.

Godin, J.-G. J., and R. W. Rangeley. 1989. Living in the fast lane: Effects of cost of locomotion on foraging behaviour in juvenile Atlantic salmon. Animal Behaviour 37:943-954.

Grant, J. W. A., and D. L. Kramer. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. Canadian Journal of Fisheries and Aquatic Sciences 47:1724-1737.

Grant, J. W. A., and D. L. G. Noakes. 1987. Movers and stayers: Foraging tactics of young-of-the-year brook charr, Salvelinus fontinalis. Journal of Animal Ecology 56:1001-1013.

Grant, J. W. A., and D. L. G. Noakes. 1988. Aggressiveness and foraging mode of young-of-the-year brook charr, Salvelinus fontinalis (Pisces, Salmonidae). Behavioral Ecology and Sociobiology 22:435-445.

Gray, D. M., and J. M. Wigham. 1973. Peak flow - rainfall event. Section VIII. IN D. M. Gray, editor. Handbook on the Principles of Hydrology. Water Information Center, Inc., Syossit, NY.

Griffith, J. S., and R. W. Smith. 1993. Use of winter concealment cover by juvenile cutthroat and brown trout in the South Fork of the Snake River, Idaho. North American Journal of Fisheries Management 13:823-830.

Grost, R. T., and W. A. Hubert. 1990. Redd site selection by brown trout in Douglas Creek, Wyoming. Journal of Freshwater Ecology 5:365-371.

Grost, R. T., and W. A. Hubert. 1991. Description of brown trout redds in a mountain stream. Transactions of the American Fisheries Society 120:582-588.

Hawkins, C. P., and ten coauthors. 1993. A hierarchical approach to classifying stream habitat features. Fisheries (Bethesda) 18(6):3-12.

Heggenes, J., and T. Traaen. 1988. Downstream migration and critical water velocities in stream channels for fry of four salmonid species. Fish Biology 32:717-727.

Heggenes, J., O. M. W. Krog, O. R. Lindas, J. G. Dokk, and T. Bremnes. 1993. Homeostatic behavioural responses in a changing environment: Brown trout (Salmo trutta) become nocturnal during winter. Journal of Animal Ecology 62:295-308.

Hewett, S. W., and B. L. Johnson. 1992. Fish bioenergetics model 2: An upgrade of a generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin Sea Grant Institute, WIS-SG-92-250, Madison, WI.

Hill, J. 1989. The Energetic Significance of Microhabitat Use in Two Stream Fishes. Ph.D. dissertation, University of Georgia, Athens, GA.

Hill, J., and G. D. Grossman. 1993. An energetic model of microhabitat use for rainbow trout and rosyside dace. Ecology 74:685-698.

Hughes, N. F., and L. M. Dill. 1990. Position choice by drift-feeding salmonids: Model and test for arctic grayling (Thymallus arcticus) in subarctic mountain streams, interior Alaska. Canadian Journal of Fisheries and Aquatic Sciences 47:2039-2048.

Jager, H. I., D. L. DeAngelis, M. J. Sale, W. Van Winkle, D. D. Schmoyer, M. J. Sabo, D. J. Orth, and J. A. Lukas. 1993. An individual-based model for smallmouth bass reproduction and young-of-year dynamics in streams. Rivers 4:91-113.

Jenkins, T. M. 1969. Social structure, position choice and micro-distribution of two trout species (Salmo trutta and Salmo gairdneri) resident in mountain streams. Animal Behavior Monographs 2:56-123.

Keeley, E. R., and J. W. A. Grant. 1993. Asymmetries in the expected value of food do not predict the outcome of contests between convict cichlids. Animal Behavior 45:1035-1037.

Kondolf, G. M., G. F. Cada, and M. J. Sale. 1987. Assessing flushing-flow requirements for brown trout spawning gravels in steep streams. Water Resources Bulletin 23:927-935.

Lam, T. J. 1988. Environmental influences on gonadal activity in fish. pp. 65-116. IN W. S. Hoar, D. J. Randall, and E. M. Donaldson, editors. Fish Physiology, Volume IX, Reproduction, Part B: Behavior and Fertility Control. Academic Press, New York.

Leitritz, E., and R. C. Lewis. 1980. Trout and salmon culture (hatchery methods). Fish Bulletin 164. California Department of Fish and Game, Sacramento, CA.

Mathur, D., W. H. Bason, E. J. Purdy, and C. A. Silver. 1985. A critique of the Instream Flow Incremental Methodology. Canadian Journal of Fisheries and Aquatic Sciences 42:825-831.

McCormack, J. C. 1962. The food of young trout (Salmo trutta) in two different becks. Journal of Animal Ecology 31:305-316.

McFadden, J. T., and E. L. Cooper. 1964. Population dynamics of brown trout in different environments. Physiological Zoology XXXVII:355-363.

McNicol, R. E., and D. L. G. Noakes. 1984. Environmental influences on territoriality of juvenile brook charr (Salvelinus fontinalis) in a stream environment. Environmental Biology of Fishes 10:29-42.

Milhous, R. T., M. A. Updike, and D. M. Schneider. 1989. Physical habitat simulation system reference manual—Version II. Instream Flow Information Paper No. 26. Washington, DC. U.S. Fish and Wildlife Service, Biological Report 89(16).

Moring, J. R. 1993. Effect of angling effort on catch rate of wild salmonids in streams stocked with catchable-size trout. North American Journal of Fisheries Management 13:234-237.

Moyle, P. B. 1976. Inland Fishes of California. University California Press, Berkeley, CA.

Murray, C. B., and J. D. McPhail. 1988. Effect of incubation temperature on the development of five species of Pacific salmon (Oncorhynchus) embryos and alevins. Canadian Journal of Zoology 66:266-273.

Ney, J. J. 1993. Bioenergetics modeling today: Growing pains on the cutting edge. Transactions of the American Fisheries Society 122:736-748.

Orth, D. J. 1987. Ecological considerations in the development and application of instream flow-habitat models. Regulated Rivers: Research & Management 1:171-181.

Ottaway, E. M., P. A. Carling, A. Clarke, and N. A. Reader. 1981. Observations on the structure of brown trout, Salmo trutta Linnaeus, redds. Journal of Fish Biology 19:593-607.

Puckett, K. J., and L. M. Dill. 1985. The energetics of feeding territoriality in juvenile coho salmon (Oncorhynchus kisutch). Behaviour 42:97-111.

Rand, P. S., D. J. Stewart, P. W. Seelbach, M. L. Jones, and L. R. Wedge. 1993. Modeling steelhead population energetics in Lakes Michigan and Ontario. Transactions of the American Fisheries Society 122:977-1001.

Rao, G. M. M. 1968. Oxygen consumption of rainbow trout (Salmo gairdneri) in relation to activity and salinity. Canadian Journal of Zoology 46:781-786.

Riehle, M. D., and J. S. Griffith. 1993. Changes in habitat use and feeding chronology of juvenile rainbow trout (Oncorhynchus mykiss) in fall and the onset of winter in Silver Creek, Idaho. Canadian Journal of Fisheries and Aquatic Sciences 50:2119-2128.

Riley, S. C., K. D. Fausch, and C. Gowan. 1992. Movement of brook trout (Salvelinus fontinalis) in four small subalpine streams in northern Colorado. Ecology of Freshwater Fish 1:112-122.

Rincon, P. A., and J. Lobon-Cervia. 1993. Microhabitat use by stream-resident brown trout: Bioenergetic consequences. Transactions of the American Fisheries Society 122:575-587.

Roell, M. J., and D. J. Orth. 1993. Trophic basis of production of stream-dwelling smallmouth bass, rock bass, and flathead catfish in relation to invertebrate bait harvest. Transactions of the American Fisheries Society 122:46-62

Roper, B. B., and D. L. Scarnecchia. 1995. Observer variability in classifying habitat types in stream surveys. North American Journal of Fisheries Management 15:49-53.

Rose, K. A., and J. H. Cowan, Jr. 1993. Individual-based model of young-of-the-year striped bass population dynamics. I. Model description and baseline simulations. Transactions of the American Fisheries Society 122:415-438.

Scott, D. P. 1962. Effect of food quantity on fecundity of rainbow trout, (Salmo gairdneri). Journal of the Fisheries Research Board of Canada 19:715-731.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Bulletin 184. Fisheries Research Board of Canada, Ottawa.

Seegrist, D. W., and R. Gard. 1972. Effects of floods on trout in Sagehen Creek, California. Transactions of the American Fisheries Society 101:478-482.

Shuter, B. J., J. A. MacLean, F. E. J. Fry, and H. A. Regier. 1980. Stochastic simulation of temperature effects on first year survival of smallmouth bass. Transactions of the American Fisheries Society 109:1-34.

Simonson, T. D., and W. A. Swenson. 1990. Critical stream velocities for young-of-year smallmouth bass in relation to habitat use. Transactions of the American Fisheries Society 119:902-909.

Skinner, W. D. 1985. Size selection of food by cutthroat trout, Salmo clarki, in an Idaho stream. Great Basin Naturalist 45:327-331.

Slaney, P. A., and T. G. Northcote. 1974. Effects of prey abundance on density and territorial behavior of young rainbow trout (Salmo gairdneri) in laboratory stream channels. Journal of the Fisheries Research Board of Canada 31:1201-1209.

Smith, R. W., and J. S. Griffith. 1994. Survival of rainbow trout during their first winter in the Henry's Fork of the Snake River, Idaho. Transactions of the American Fisheries Society 123:747-756.

Statzner, B., J.-M. Elouard, and C. Dejoux. 1985. Field experiments on the relationship between drift and benthic densities of aquatic insects in tropical streams (Ivory Coast). II. Cheumatopsyche falcifera (Trichoptera: Hydropsychidae). Journal of Animal Ecology 55:93-110.

Stewart, D. J. 1980. Salmonid predators and their forage base in Lake Michigan: A bioenergetics-modeling synthesis. Ph.D. Thesis, University of Wisconsin–Madison, WI.

Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsall. 1983. An energetics model for lake trout, (Salvelinus namaycush): Application to the Lake Michigan population. Canadian Journal of Fisheries and Aquatic Sciences 40:681-698.

Studley, T. K., J. E. Baldrige, L. M. Wise, A. P. Spina, E. McElravy, R. W. Smith, T. D. Yuen, L. Travanti, S. D. Chase, S. F. Railsback. 1995. Response of fish populations to altered flows project: Baseline Report (1985-1992) (Volumes I-III). Report 009.4-94.3. Pacific Gas and Electric Company, Department of Research and Development, San Ramon, CA. In press.

Sullivan, K. 1986. Hydraulics and fish habitat in relation to channel morphology. Ph.D. Thesis, The Johns Hopkins University, Baltimore.

Tanida, K, T. Maruyama, and Y. Saito. 1989. Feeding ecology of Japanese charr (Salvelinus leucomaenis) in a high moor and adjacent streams in central Japan. Physiological Ecology, Japan, Special Volume 1:279-294.

Thornton, K. W., and A. S. Lessem. 1978. A temperature algorithm for modifying biological rates. Transactions of the American Fisheries Society 107:284-287.

Timoshina, L. A. 1972. Embryonic development of the rainbow trout (Salmo gairdneri irideus (Gibb.)) at different temperatures. Journal of Ichthyology 12:425-432.

Tyler, J. A., and K. A. Rose. 1994. Individual variability and spatial heterogeneity in fish population models. Reviews in Fish Biology and Fisheries 4:91-123.

Vincent, E. R. 1987. Effects of stocking catchable-size hatchery rainbow trout on two wild trout species in the Madison River and O'Dell Creek, Montana. North American Journal of Fisheries Management 7:91-105.

Vinyard, G. L., and W. J. O'Brien. 1976. Effects of light and turbidity on the reactive distance of bluegill (Lepomis macrochirus). Journal of the Fisheries Research Board of Canada 33:2845-2849.

Ware, D. M. 1975. Growth, metabolism, and optimal swimming speed of a pelagic fish. Journal of the Fisheries Research Board of Canada 32:33-41.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15:393-425.

Winemiller, K. O., and K. A. Rose. 1992. Patterns of life-history diversification in North American fishes: Implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences 49:2196-2218.

Wise, L. M., and W. S. Lifton. 1994. Preliminary verification of habitat suitability criteria on three central Sierra streams. Prepared for Southern California Edison Company, Rosemead, CA, by ENTRIX, Walnut Creek, CA.

Wismer, D. A., and A. E. Christie. 1987. Temperature relationships of Great Lakes fishes: A data compilation. Great Lakes Fishery Commission, Special Publication No. 87-3, Ann Arbor, MI.

Witzel, L. D., and H. R. MacCrimmon. 1983. Redd-site selection by brook trout and brown trout in southwestern Ontario streams. Transactions of the American Fisheries Society 112:760-771.

APPENDIX 1 INPUT PARAMETERS

The following seven tables give the names of the model input parameters used in the report, the names used in the FORTRAN computer code, the values used in calibrating the model for the baseline simulation (Sect. 9), and definitions. There is a table for each of Sects. 2–8. The names of the parameters used in each section are listed in alphabetical order in these appendix tables.

APPENDIX 1-1 PARAMETERS FOR PHYSICAL HABITAT

Parameter name used in the report and in the FORTRAN computer code, value for the baseline simulation, and definition for the parameters relating to physical habitat (see Sect. 2). An x in the column headed "A" means that the parameter value is based directly or indirectly on data from Segment 8 of the North Fork Middle Fork Tule River, CA. An x in the column headed "B" means that simulation results on habitat use, growth, and/or mortality are relatively sensitive to the value for this parameter.

Parameter Name					
Report	Code	Value	A	B	Definition
a_{Vmax} , b_{Vmax}	vmaxa, vmaxb	56.3, 1.59			Parameters of the equation for maximum water column velocity as a function of average water column velocity.
b_{vel}	beta	−0.5			Exponent for adjusting velocity for differences in depth between donor and receptor cells.
b_{Vmax}	bvmax	2.5			Maximum value for the exponent in the equation relating velocity to flow at high flows.
F_{bot}	vbed	0.67			Ratio of the velocity at 4 cm above the bottom to the average water column velocity for each cell; used in calculating benthic foraging velocity.
f_{cov}	tcover	0.3			Adjustment factor for fraction of the area of a habitat unit with instream cover.
f_{spawn}	fspawn	10		X	Adjustment factor for fraction of the area of a habitat unit suitable for spawning; value is selected during calibration to control frequency of superimposition.
I_{simQ}	isimq	0, 1			Switch for inputting a daily time series of flow data (= 0) or simulating daily flow (= 1).
I_{simT}	isimt	0, 1			Switch for inputting a daily time series of temperature data (= 0) or simulating daily temperature (= 1).
$\bar{L}_{cov}$	XL50	100			Median length (mm) of instream cover objects.
N_{min}	mnmin	0.001		X	Value for Manning's N when flow exceeds bankfull flow (Q_{max}).
N_{minQ}	mincal	3			Minimum number of PHABSIM calibration flows when a cell is wetted that are required in order to use the velocity-flow rating curve to estimate the velocity for that cell.
Q_{base}	qbase	0.0	X		Imposed minimum instream flow (cfs).
Q_{max}	qmax	800	X		Maximum flow (cfs) for valid extrapolation of the PHABSIM methodology.
Q_{set}	qset	5			Constant value of flow (cfs) used when simulating the daily flow regime (I_{simQ} = 1).

Parameter Name					
Report	Code	Value	A	B	Definition
S_{ave}	slavg	0.055	X		Average gradient for the entire stream segment.
S_{min}, S_{max}	wsmin(i), wsmax(i)	0.00, 0.01 0.02, 0.06 0.02, 0.06 0.01, 0.02			Minimum and maximum water surface slope for each habitat type (i); 1=pool, 2=riffle, 3=pocket water, 4=run.
T_{ave}	tavg	16.2	X		Average water temperature (°C) for the water year when the temperature regime is simulated ($I_{simT} = 1$).
T_{max}	tmax	30.0	X		Maximum water temperature (°C) during the water year when the temperature regime is simulated ($I_{simT} = 1$).
t_{Tave}	tavday	115	X		Calendar day when water temperature first equals the average water temperature (T_{ave}).
V_{add}	vaddp	1.59			Parameters of the equation for maximum water column velocity as a function of average water column velocity for pool habitat units .
V_{cap}	velcap	2.5			Maximum value for estimated velocity (m/s) in a cell.

APPENDIX 1-2 PARAMETERS FOR SPAWNING

Parameter name used in the report and in the FORTRAN computer code, value for the baseline simulation, and definition for the parameters relating to spawning (see Sect. 3). Values are given for brown trout (i=1 for BT) and rainbow trout (i=2 RT); stocked hatchery rainbow trout (i=3 for HRT) have the same parameter values as native rainbow trout unless otherwise indicated. Parameter values are the same for all trout unless indicated otherwise. An x in the column headed "A" means that the parameter value is based directly or indirectly on data from Segment 8 of the North Fork Middle Fork Tule River, CA. An x in the column headed "B" means that simulation results on habitat use, growth, and/or mortality are relatively sensitive to the value for this parameter.

Parameter Name					
Report	Code	Value	A	B	Definition
a_{fec} , b_{fec}	feca, fecb	BT: 1.16, 2.54 RT: 1.16, 2.54			Parameters of the equation for fecundity as a function of female length.
D_{move}	demove	BT: 1.5 RT: 1.5		X	Minimum water depth for spawning and for a PHABSIM cell to be habitable as a fraction of the length of the trout
F_{eggs}	fracfec	BT: 0.9 RT: 0.9			Fraction of the number of mature eggs produced by a female that are successfully fertilized and deposited in a redd.
f_{spawn}	fspawn	10		X	Adjustment factor for fraction of the area of a habitat unit suitable for spawning.
J_{sp1} , J_{sp2}	spawnb(i), spawne(i)	BT: Oct 1-Dec 31 RT: Apr 1-Jun 30			Calendar days for the start and end of the spawning season.
K_{sp}	cfspawn	BT: 0.6 RT: 0.6			Minimum condition factor on day of spawning required for spawning.
L_{mat}	sizmat(i)	BT: 170 RT: 130		X	Minimum length (mm FL) for sexual maturity.

Parameter Name					
Report	Code	Value	A	B	Definition
L_{spawn}	psp12(i)	BT: 210 RT: 170		X	Length (mm FL) at and above which the probability of spawning is 1.0.
P_{onesp}	onespawn	BT: 1.0 RT: 1.0			Proportion of females spawning on only one day.
Q_{spmax}	qmax	BT: 800 RT: 800	X		Maximum daily flow (cfs) above which a female trout scheduled to spawn on that day delays spawning until a later day.
ΔQ_{max}	dqmax	BT: 0.1 RT: 0.1			Threshold for relative change in daily flow above which a female scheduled to spawn on that day delays spawning until a later day.
T_{spmin} , T_{spaw2}	tspaw1(i), tspaw2(i)	BT: 4.0, 10.0 RT: 8.0, 13.0			Minimum and maximum temperature (°C), respectively, for spawning.

APPENDIX 1-3 PARAMETERS FOR DEVELOPMENT AND MORTALITY IN THE REDD

The name of parameters used in the report and in the FORTRAN computer code, value for the baseline simulation, and definition for the parameters relating to development and mortality in the redd (see Sect. 4). Values are given for brown trout (i= 1 for BT) and rainbow trout (i=2 for RT); stocked hatchery rainbow trout (i = 3 for HRT) have the same parameter values as native rainbow trout unless indicated otherwise. Parameter values are the same for all age trout unless indicated otherwise. A "X" in the column headed "A" means that the parameter value is based directly or indirectly on data from Segment 8 of the North Fork Middle Fork Tule River, CA. A "X" in the column headed "B" means that simulation results on habitat use, growth, and/or mortality are relatively sensitive to the value for this parameter.

Parameter Name					
Report	Code	Value	A	B	Definition
a_{dev} , b_{dev} , c_{dev}	adev(i), bdev(i), cdev(i)	BT: 0.00313, 0.0000307, 0.0000934 RT: −0.000253, 0.00134; 0.0000321			Parameters of the equation for daily development rate of eggs and alevins as a function of temperature.
A_{redd}	reddarea	BT: 0.3 RT: 0.3			Average area of a redd (m^2).
D_{dewat}	dminredd	BT: 0.0 RT: 0.0			Minimum water depth (m) for a redd to not be dewatered.
f_{spawn}	fspawn	BT: 10 RT: 10		X	Adjustment factor for fraction of the area of a habitat unit suitable for spawning.
F_{lost}	ppocket	BT: 0.5 RT: 0.5			Fraction of eggs and alevins lost from an existing redd due to superimposition.
$L_{♀1}$, L_{fry1} ; $L_{♀2}$, L_{fry2}	sizmat(i), lfrymin; lfmax(i), lfrymax	BT: 170,20; 300,30 RT: 130,20; 220,30			Coordinates of the two points defining the straight line relating length of fry at emergence to female length. $L_{♀1}$ is the length at first maturity.
P_{bkgd}	bkgrd1(i)	BT: 0.004 RT: 0.010		X	Daily risk of mortality of eggs and alevins due to unspecified, density-independent sources of mortality. Values determined during calibration for the baseline simulation.
P_{dewat}	dewatr	BT: 0.4 RT: 0.4			Daily risk of mortality for eggs and alevins due to dewatering of the cell in which the redd is located.
$RSUM1_{dev}$	rdevet	BT: 0.95 RT: 0.95			Emergence of fry from a redd starts on the day that $RSUM_{dev}$ reaches this threshold.

Parameter Name		Value	A	B	Definition
Report	Code				
T_1 , T_2 , T_3 , T_4	tm(1,i), tm(2,i), tm(3,i), tm(4,i)	BT: −4.0, 0.5, 11.0, 16.0 RT: −2.0, 5.0, 15.5, 21.0		X	Four temperature parameters (°C) defining the equation for risk of mortality as a function of temperature for eggs and alevins.
V_{ave1} , P_{sc1} ; V_{ave2} , P_{sc2}	vave1, scour1; vave2, scour2	BT: 0.9, 0.01; 1.6, 0.95 RT: 0.9, 0.01; 1.6, 0.95		X	Coordinates of the two points defining the logistic function relating water velocity (m/s) to daily risk of mortality for eggs and alevins due to scouring.

APPENDIX 1-4 PARAMETERS FOR GROWTH: FORAGING AND CONSUMPTION

The name of parameters used in the report and in the FORTRAN computer code, value for the baseline simulation, and definition for the parameters relating to foraging and consumption (see Sect. 5). Values are given for brown trout ($i = 1$ for BT) and rainbow trout ($i = 2$ for RT); stocked hatchery rainbow trout ($i = 3$ for HRT) have the same parameter values as native rainbow trout unless indicated otherwise. Parameter values are the same for all age trout unless indicated otherwise. A "X" in the column headed "A" means that the parameter value is based directly or indirectly on data from Segment 8 of the North Fork Middle Fork Tule River, CA. A "X" in the column headed "B" means that simulation results on habitat use, growth, and/or mortality are relatively sensitive to the value for this parameter.

Parameter Name					
Report	Code	Value	A	B	Definition
a_{cal}	calaf, calyf	1400, 1000			Conversion factor (cal/g) between calories and grams wet weight for Age 1 and older trout and for Age 0 trout, respectively.
a_{Cmax}, b_{Cmax}	cmaxa, cmaxb	BT: 0.60, 0.76 RT: 0.60, 0.76			Parameters of weight-dependence for maximum consumption.
a_{RD}, b_{RD}, c_{RD}, d_{RD}	rda, rdb, rdc, rdd	BT: 5.91, 0.847, 0.0473, 1.74 RT: 5.91, 0.847, 0.0473, 1.74		X	Parameters for reactive distance as a function of temperature, average water column velocity, and length of the trout.
a_{swim}, b_{swim}, c_{swim}	speedm, speedb1, speedc	BT: 44.1, 0.128, 0.0405 RT: 44.1, 0.128, 0.0405			Parameters for maximum swim speed as a function of the weight of the trout and temperature.
a_{Vmax}, b_{Vmax}	vmaxa, vmaxb	56.3, 1.59		X	Parameters of the equation for maximum water column velocity as a function of average water column velocity.
d_{swim}, e_{swim}, f_{swim}	≤ 150 g wet wt: speeda0, speedb0, speedc > 150 g wet wt: speeda1, speedb1, speedc	BT: 2.84, 0.485, 0.0405 RT: 2.84, 0.485, 0.0405 BT: 9.70, 0.128, 0.0405 RT: 9.70, 0.128, 0.0405			Parameters for optimal swim speed as a function of the weight of the trout and temperature.

Parameter Name		Value	A	B	Definition
Report	Code				
f(T)	t(i,j), tk(i,j)	BT: T,°C f(T) 7.0 0.20 15.0 0.70 18.0 0.98 21.0 0.20 RT: T,°C f(T) 4.0 0.20 15.0 0.70 22.0 0.98 24.0 0.20			Temperature-dependent function multiplying weight-dependent maximum consumption. Defining the function requires specifying [T, f(T)] coordinates for four points.
f_B	pcba	BT: 12 RT: 12		X	Adjustment factor for fraction of benthic prey available to a trout foraging on the stream bottom. Values are determined during calibration for the baseline simulation.
f_{dem}	demin	BT: 0.15 RT: 0.15		X	Parameter for the maximum number of hours a trout is active as a function of its weight (i.e., a demand function for foraging).
F_{fish}	pfish	BT: 0.0 RT: 0.0			Fraction of prey consumed that are fish. (1.0 - P_{fish}) is the fraction of prey consumed that are invertebrates and Age 0 fish.
F_{prey1} , F_{prey2}	cali, calyf	600, 1000			Conversion factors between grams wet weight and calories for invertebrate prey and Age 1 and fish prey , respectively.
$F0_{Cmax}$, $F1_{Cmax}$	psety, pseta	User's choices between 0 and 1			Fraction of maximum consumption for Age 0 trout and Age 1 and older trout, respectively. These parameters are used in the nonforaging option.
m_{drift}	pcbb	11		X	Parameter for average supply rate of drifting prey.
N_B	preyben	0.0013			Average biomass density (g/cm^2) of benthic prey on the stream bottom.
RD_{max}	rdmax	BT: 5 RT: 5			Maximum reactive distance (body lengths).
T_{crit}	tcrit1	BT: 3.0 RT: 3.0			Critical lower temperature (°C) for foraging and activity respiration.

APPENDIX 1-5 PARAMETERS FOR GROWTH: ENERGETIC COSTS

The name for parameters used in the report and in the FORTRAN computer code, value for the baseline simulation, and definition for the parameters relating to energetic costs (see Sect. 6). Values are given for brown trout (i = 1 for BT) and rainbow trout (i = 1 for RT); stocked hatchery rainbow trout (i = 3 for HRT) have the same parameter values as native rainbow trout unless indicated otherwise. Parameter values are the same for all age trout unless indicated otherwise. A "X" in the column headed "A" means that the parameter value is based directly or indirectly on data from Segment 8 of the North Fork Middle Fork Tule River, CA. A "X" in the column headed "B" means that simulation results on habitat use, growth, and/or mortality are relatively sensitive to the value for this parameter.

Parameter Name					
Report	Code	Value	A	B	Definition
a_{cal}	calaf, calyf	1,400, 1000			Conversion factor (cal/g) between calories and grams wet weight for Age 1 and older trout and for Age 0 trout, respectively.
a_{eg} , b_{eg} , c_{eg}	ega, egb, egc	BT: 0.212, −0.222, 0.631 RT: 0.212, −0.222, 0.631			Parameters of the equation for egestion.
a_{ex} , b_{ex} , c_{ex}	exa, exb, exc	BT: 0.0314, 0.580, −0.299 RT: 0.0314, 0.580, −0.299			Parameters of the equation for excretion.
a_L , b_L	la(i), lb(i)	BT: 0.0000132, 2.97 RT: 0.0000147, 2.96	X		Parameters of the equation relating expected wet weight (g) of a trout to its length (mm FL).
a_R , b_R , c_R	ra(i), rb(i), rc(i)	BT: 7.13, 0.784, 0.0693 RT: 7.13, 0.784, 0.0693			Parameters of the equation for standard respiration.
a_{SDA}	sa	BT: 0.14 RT: 0.14			Proportion of a trout's assimilated energy that is used for subsequent biochemical transformations.
d_R	sfact	BT: 0.030 RT: 0.030			Parameter in the equation for activity respiration for the dependence on water velocity or swimming speed.
d_{vcov}	dvcov	BT: 5.6 RT: 5.6			Difference between strike and focal velocity for a trout foraging from a feeding station.
T_{crit}	tcrit1	BT: 3.0 RT: 3.0			Critical lower temperature (°C) for foraging and activity respiration
X_{fish}, X_{inv}	xkfish, xkinv	0.033, 0.10			Fraction of the wet weight of a fish prey item or an invertebrate prey item, respectively, that is indigestible

APPENDIX 1-6 PARAMETERS FOR HABITAT USE AND MOVEMENT

The name for parameters used in the report and in the FORTRAN computer code, value for the baseline simulation, and definition for the parameters relating to habitat use and movement (see Sect. 7). Values are given for brown trout (i=1 for BT) and rainbow trout (i=2 for RT); stocked hatchery rainbow trout (i=3 for HRT) have the same parameter values as native rainbow trout unless indicated otherwise. Parameter values are the same for all age trout unless indicated otherwise. A "X" in the column headed "A" means that the parameter value is based directly or indirectly on data from Segment 8 of the North Fork Middle Fork Tule River, CA. A "X" in the column headed "B" means that simulation results on habitat use, growth, and/or mortality are relatively sensitive to the value for this parameter.

Parameter Name					
Report	Code	Value	A	B	Definition
a_{stat} , b_{stat}	terra, terrb	BT: 3.55E-6, 2.61 RT: 3.55E-6, 2.61			Parameters for area of a trout's feeding station as a function of trout length.
c_{stat}	tspacey, tspacea	BT: 0.17 (Age 0), 0.15 (Age 1+) RT: 0.17 (Age 0), 0.15 (Age 1+)		X	Adjustment factor for total feeding area available in a habitat unit; value determined in calibrating for the baseline simulation.
d_{move}	demove	BT: 1.5 RT: 1.5			Fraction of a trout's length required for its current cell to be habitable in terms of depth.
f_{cov}	tcover	0.3			Adjustment factor for fraction of the area of a habitat unit with instream cover; value determined during calibration for the baseline simulation.
f_{mem}	memfac	BT: 0.5 RT: 0.5			Memory factor used in calculating a trout's expectation of mortality risk and energetic status.
P_{move}	pmove	BT: 0.01 RT: 0.01			Probability of a trout moving from its current cell due to unspecified reasons (i.e., stochastic movement or exploratory behavior).
T_{tmin} , T_{tmax}	tlhide(i), tuhide(i)	BT: 6.0, 19.0 RT: 8.0, 21.0			Minimum and maximum temperature (°C), respectively, below which and above which feeding stations are not a contested resource.
v_{spec}	domfac(i)	BT: 1.0 RT: 0.8 HRT: 0.5			Weighting factor for species; used in dominance ranking for access to feeding stations and cover. Values are determined in calibrating the model for the baseline simulation.

APPENDIX 1-7 PARAMETERS FOR MORTALITY

The name for parameters used in the report and in the FORTRAN computer code, value for the baseline simulation, and definition for the parameters relating to mortality (see Sect. 8). Values are given for brown trout (i=1 for BT) and rainbow trout (i=2 for RT); stocked hatchery rainbow trout (i=3 for HRT) have the same parameter values as native rainbow trout unless indicated otherwise. Parameter values are the same for all age trout unless indicated otherwise. A "X" in the column headed "A" means that the parameter value is based directly or indirectly on data from Segment 8 of the North Fork Middle Fork Tule River, CA. A "X" in the column headed "B" means that simulation results on habitat use, growth, and/or mortality are relatively sensitive to the value for this parameter.

Parameter Name					
Report	Code	Value	A	B	Definition
a_{swim} , b_{swim} , c_{swim}	speedm, speedb1, speedc	BT: 44.1,0.128,0.0405 RT: 44.1,0.128,0.0405			Maximum swim speed as a function of trout weight and temperature.
J_{fish1} , J_{fish2}	angbeg, angend	April 27, September 30	X		Beginning date (average) and end date of the fishing season.
D_{die}	dedie	BT: 0.25 RT: 0.25			Minimum depth as a fraction of a trout's length; used in representing the probability of stranding.
f_{day}	hooky	Mon-Thu: 0.85 Fri-Sun: 1.0	X		Adjustment factor for fishing mortality for weekdays and for weekends and holidays.
f_{hook}	hookmort	BT: 0.1 RT: 0.1			Adjustment factor for fishing mortality for hook & release.
f_{keep}	keepfac	BT: 0.4 RT: 0.4 HRT: 0.8			Adjustment factor for fishing mortality for probability of keeping a caught fish.
f_{month}	mofac(1), ... , mofac(12)		X		Adjustment factor for fishing mortality for month.
f_{spec}	spf(i)	BT: 0.02 RT: 0.04 HRT: 1.0	X		Adjustment factor for fishing mortality for differences in catchability among species.
F_{Lmax}	prdbig	BT: 0.001 RT: 0.001			Value of the Y-axis coordinate corresponding to the L_{max} parameter in length-dependent factor of the equation for P_{mort}.
K_{min}	cfmin	BT: 0.5 RT: 0.5			Minimum condition factor required for survival.
L_{min} , L_{max}	lfrymin, lrskbig	BT: 20, 350 RT: 20, 350		X	Length (mm) parameters in the length-dependent factor of the equation for P_{mort}.

Parameter Name		Value	A	B	Definition
Report	Code				
N_1 , f_{dens1} ; N_2 , f_{dens2}	dens1, ddfac1; dens2, ddfac2	100, 0.20; 200, 0.95			Coordinates of two points (N is number of trout per 100 m of stream length; f_{dens} is a unitless factor between 0.0 and 1.0) defining the density-dependent adjustment factor for fishing mortality.
P_{fmax}	pfmax	BT: 1.0 RT: 1.0		X	Maximum daily probability of fishing mortality.
PS_{HRT}	phatch	0.848	X		Expected daily probability of survival for hatchery rainbow trout.
P_{repm}	repmort(i)	BT: 0.6 RT: 0.6		X	Risk of mortality due to reproduction.
P_{strand}	pstrand	BT: 0.5 RT: 0.5			Daily probability of mortality due to being stranded.
T_{CTM}	ctm0(i), ctm1(i)	BT: 24.0 (Age 0); 20.0 (Age 1) RT: 26.0 (Age 0): 22.0 (Age 1)			Temperature (°C) at and above which a trout dies.
Z_{act}	prdint	BT: 0.02 RT: 0.02			Daily instantaneous mortality rate for those risks present primarily when a trout is active; value determined in calibrating the model for the baseline simulation.
Z_{24}	z24	BT: 0.001 RT: 0.001			Daily instantaneous mortality rate for those risks present 24 hours a day; value determined in calibrating the model for the baseline simulation.

APPENDIX 2 LIFE HISTORIES

The following text is taken verbatim from Inland Fishes of California by P. B. Moyle (1976, pp. 129-132 for rainbow trout and pp. 142-144 for brown trout). See his book for references cited below.

Rainbow Trout (Oncorhynchus mykiss)

Life History. The life-history patterns of rainbow trout range from the highly migratory, sea-going pattern of steelhead populations, to the pattern of many isolated populations in small streams, where an individual trout may complete its entire life cycle in a few hundred meters of stream. When in fresh water, most rainbow trout are found in cool, clear, fast-flowing permanent streams and rivers, where riffles tend to predominate over pools. In the Sacramento-San Joaquin system they also inhabit the Squawfish-sucker-hardhead Zone in the larger streams, even though temperatures may often approach the maximum they can withstand. Mountain lakes and the cold, deep waters of reservoirs also provide suitable habitat for rainbow trout, but such populations have to be artificially maintained if suitable spawning streams are lacking. Rainbow trout will survive temperatures of 0 to 28°C. They can withstand temperatures at the upper end of this range, however, only if they have been gradually acclimated to them and if the water is saturated with oxygen. Optimum temperatures for growth and for completion of most stages of their life history seem to be 13 to 21°C. At low temperatures, they can withstand oxygen concentrations as low as 1.5 to 2.0 ppm but normally concentrations close to saturation are required for growth. Their tolerance of the varying chemical conditions of water is also broad. They can live in water ranging in pH from 5.8 to 9.6. All other factors being equal, best growth seems to be achieved in slightly alkaline waters (pH of 7 to 8), although Eagle Lake trout have adapted to the highly alkaline waters of Eagle Lake (pH of 8.4 to 9.6).

While rainbow trout are the only fish species found in many California streams, more often than not they occur with other salmonids (especially brown trout and juvenile coho and chinook salmon), sculpins (Cottus spp.), speckled dace, suckers (Catostomus spp.), and Sacramento squawfish. It is unusual, however, to find more than three to four other species in abundance where rainbow trout are common. Rainbow trout are fairly flexible in their behavior and habitat requirements. They can interact successfully with other species of fish, avoiding as much as possible direct competition for food and space. In coastal streams, juvenile steelhead interact with juvenile coho and chinook salmon and, as a result, the species select different microhabitats (Hartman, 1965; Everest and Chapman, 1972). When brown trout and rainbow trout are found in the same stream, brown trout tend to select slow, deep pools with lots of cover, while rainbow trout select the faster water (Lewis, 1969). Rainbow trout also tend to feed more on drift organisms, while brown trout feed on the bottom. The interactions between rainbow trout and various nongame species are discussed in the ecology chapter of this book.

One of the main reasons rainbow trout are so successful at interacting with other fish species is that they are highly aggressive and defend feeding territories in streams. Other salmonids recognize the aggressive displays of rainbow trout (e.g., rigid swimming, flared operculae, nipping at the caudal peduncle of invading fish) and usually react either by fleeing or by challenging the trout with similar displays, perhaps driving it off its territory. The winners of such interspecific contests are determined by a number of factors, but relative size and habitat preferences play leading roles. Rainbow trout can generally drive nongame fishes such as suckers and squawfish, which do not respond to the displays themselves, from feeding territories by repeatedly rushing at the invaders and nipping at their sides and caudal peduncles (H. Li, pers. comm.).

Territorial displays are also extremely important in the intraspecific interactions of rainbow trout. In streams, rainbow trout set up feeding territories which they defend from each other. The number of territories depends on many factors, but probably the most important are size of the fish, speed of current, water temperature, and availability of cover. Superimposed on this territorial mosaic, however, is a dominance hierarchy in which larger fish are dominant over small fish and hold much larger territories. The smaller fish may actually hold small territories within the territory of the large fish. They interact with each other and a stable hierarchy develops to the point where they will actually help the dominant trout defend the entire territory against invading trout (Jenkins, 1969). These territorial interactions may be the most important factor limiting the number of trout in many streams, outweighing food availability.

The competitive interactions of rainbow trout with each other and with other fish species in lakes is less well understood than it is in streams. The trout tend to school and wander about within lakes, so aggressive behavior probably plays a minor role. The numerous observations of decrease in trout growth rates and population size following the introduction of another species (usually a cyprinid) into a pure trout lake, indicates, however, that direct competition for limited food resources takes place initially. Eventually, the trout and the new species will segregate by habitat and feeding strategies and the trout may subsist in part by preying on the other species. A classic, well-documented case of this sort is Paul Lake, British Columbia (Johannes and Larkin, 1961).

In the summer months, stream-dwelling rainbow trout feed mostly on drift organisms, but they will also take active bottom invertebrates. Thus, the stomachs from a sample of trout taken from one stream at the same time are likely to contain a hodgepodge of terrestrial insects, adult and emergent aquatic insects, aquatic insect larvae, amphipods, snails, and occasional small fish. Individual trout, however, tend to specialize in the type of organisms they feed on, even over a long period of time, and do not take the whole range of foods available (Bryan and Larkin, 1972). In the winter, feeding is considerably reduced over summer levels and the trout feed mostly on bottom-dwelling invertebrates. The most commonly taken bottom invertebrates at all seasons are either those that drift on a regular basis (e.g., baetid mayfly larvae, amphipods), those that are active bottom crawlers or live in exposed positions, or those that are large in size. The size of the organism taken tends to increase with the size of the feeding fish. Rainbow trout can feed at virtually any hour of the day or night but feeding activity is usually most intense around dusk.

In lakes, feeding varies with invertebrate availability. Although benthic invertebrates and zooplankton seem to be preferred, terrestrial insects will be taken in numbers when other foods are scarce. Rainbow trout in lakes also have a greater proclivity for feeding on fish than do stream-dwelling rainbows, although fish normally do not become an important item in the diet until the trout are 30 to 35 cm TL. Thus, large Eagle Lake trout subsist mostly on tui chubs, while trout in California reservoirs subsist on threadfin shad or delta smelt. Other fishes commonly eaten in California are sculpins and suckers. As in streams, feeding is most intense during the summer but can continue throughout the winter, at temperatures as low as 1°C (Elliott and Jenkins, 1972). Steelhead feed on estuarine invertebrates after they leave their home streams but fish gradually become more important in their diet as they increase in size. The large size and rapid growth achieved by steelhead, and to a lesser extent by lake-dwelling rainbow trout, can be attributed in a large part to their diet of fish.

Growth rates in rainbow trout are variable. In mountain lakes, they reach 11 to 17 cm TL in their first year,14 to 21 cm TL in their second, and 20 to 23 cm TL in their third. In such lakes they seldom live longer than six years or grow over 40 cm TL. Growth rates are similar in small California streams. The most rapid growth in California is achieved in large lakes and reservoirs. In Eagle Lake, trout 20 to 23 cm TL are one year old, 43 to 46 cm TL are two years old, and 46 to 56 cm TL are three years old. Similar growth is achieved by fish planted as fingerlings in some reservoirs (e.g., Crowley Lake, Mono County) but generally it is somewhat slower, especially after the first year. Juvenile steelhead migrate out to sea at one to three years of age, at 13 to 25 cm TL. After one to two years at sea they return at 38 to 69 cm TL (1.4 to 5.4 kg). The largest known nonsteelhead rainbow trout, from Jewel Lake, British Columbia, weighed 23.9 kg (Hart,1973), although the largest caught by angling (from Lake Pend Oreille, Idaho) weighed 16.8 kg. The largest such fish from California (Feather River) weighed 9.6 kg, while the largest California steelhead known (Smith River) weighed 9.7 kg (Anonymous, 1964). The largest steelhead on record, from Alaska, weighed 19.1 kg (Hart,1973). The oldest rainbow trout known are those from Eagle Lake, at eleven years. Steelhead occasionally reach nine years old, but the maximum age for most nonsteelhead rainbow trout is seven years.

Most nonanadromous rainbow trout mature in their second or third year, but the time of first maturity can vary from the first to the fifth year of life. Mature fish can be of any size from 13 cm on up. Most steelhead spawn for the first time after spending two to three years in fresh water and then one to two years in salt water. However, spawning fish, usually small males, that have spent only one year in each habitat do occur on a regular basis in some streams.

Most wild rainbow trout are spring spawners, from February to June, but low temperatures in high mountain areas may delay spawning until July or August. California steelhead trout also spawn in the spring, but they frequently migrate upstream in the fall several months before they actually spawn. In some north-coast streams, small numbers migrate upstream in the late spring, spend the summer in deep pools, and spawn in the spring of the following year. Steelhead and other rainbow trout have well-developed homing abilities, and usually spawn in the same stream and area in which they had lived as fry. This means that local races of trout tend to develop that are adapted to local conditions.

Successful reproduction of rainbow trout generally requires a gravel riffle, in which a redd can be dug by the female and the eggs successfully incubated. Spawning behavior is similar to that of brown trout. The number of eggs laid per female depends on the size and origin of the fish but ranges from 200 to 12,000 eggs. Rainbow trout under 30 cm TL typically contain less than 1,000 eggs, while steelhead contain about 2,000 eggs per kg of body weight. Both rainbow and steelhead usually spawn once a year, but it is not unusual for fish to skip a year between spawnings.

The eggs hatch in three to four weeks (at 10 to 15°C) and the fry emerge from the gravel two to three weeks later. The fry initially live in quiet waters close to shore and exhibit little aggressive behavior for several weeks.

Status. Rainbow trout are the most popular and widely distributed gamefish in California. The demand for them is far beyond the natural reproductive capacities of wild populations, so a considerable portion of the fishing-license revenues of the California Department of Fish and Game goes towards supporting hatcheries that rear domestic strains of rainbow trout for planting on a put-and-take basis. Most trout planted are 18 to 20 cm TL and are caught within two weeks of planting (Butler and Borgeson, 1965). This is fortunate because hatchery-raised fish are illadapted for surviving in streams and are likely to die of starvation or stress within a few week anyway. Mortality is highest when they are planted in relatively small numbers in a stream tha also sustains a wild trout population, because the planted fish will be unable to break into the established dominance hierarchies of the wild trout. If large numbers are planted over a wild trou population, the effect of the sheer numbers is likely to disrupt the established hierarchies, making the wild fish more vulnerable to angling. Such streams generally have to be continually planted if any sort of trout fishery is to be sustained, since neither the wild nor domestic trout can maintain themselves very easily.

In lakes, the survival rates of planted fish are much higher than they are in streams because of the absence of dominance hierarchies in wild fish, the low expenditure of energy required to stay alive (and become adjusted to the environment) in the absence of current, and the lower vulnerability of the fish to angling. In lakes, it is often economical to plant fingerling trout in place of catchable size fish, which it seldom is in streams.

Despite the generally low survival rates of planted trout, especially in streams, a few often will survive and interbreed with wild trout. Thus, indiscriminate planting of rainbow trout has led to loss through hybridization of many distinctive local populations, not only of rainbow trout but of other closely related species such as golden trout, cutthroat trout, and redband trout. Only in recent years has the aesthetic value of distinctive local populations been recognized and efforts made to preserve the few that are still left.

Another problem of some concern to fisheries managers in California is the long-term decline of steelhead populations. The decline is largely attributable to degradation of the spawning streams through sloppy logging, dewatering, dam construction, and pollution. Hatchery production of young steelhead can compensate in part for the loss of naturally spawned fish but it cannot compensate for the loss of the streams.

Brown Trout (Salmo trutta)

Life History. Brown trout, because they are the trout of Europe and a favorite sport fish of serious anglers the world over, are perhaps the most studied of the trouts and chars, as is indicated by the accounts of Staley (1966), Frost and Brown (1967), Carlander (1969), and Scott and Crossman (1973). Adult brown trout are largely bottom-oriented pool dwellers but younger, smaller trout are as likely to be found in riffles as in pools. The optimum habitat for brown trout seems to be medium to large sized, slightly alkaline, clear streams with both swift riffles and large, deep pools. They are found, however, in the complete range of trout waters from spring-fed trickles to large lakes. Anadromous brown trout are rare in California (Fry, 1973). Temperature is an important factor limiting their distribution. They can survive for short periods of time at temperatures in excess of 27°C but the most rapid growth occurs between 7 and 19°C. They seem to prefer, however, temperatures in the upper half of this range. Vincent and Miller (1969) found that they would not move into the upper reaches of Colorado streams unless water temperatures exceeded 13°C for extended periods of time.

In streams, nonreproducing brown trout are rather sedentary, seldom moving more than a few meters from one spot. Trout less than 25 cm TL set up feeding territories and a dominance hierarchy is usually established among the fish in one area. The largest, most aggressive fish defends the largest territory, which is usually located in one of the best positions in the stream for cover and food availability. Trout larger than 25 cm TL are more mobile and tend to remain under cover (undercut banks, logs, etc.) during the day, coming out to actively pursue prey during the evening. Even these large fish, however, generally patrol rather restricted areas (Jenkins, 1969).

The food of brown trout in streams changes with their size and the season. In general, the smaller the trout, the greater percentage of its diet will be made up of drift organisms, especially terrestrial insects. As the trout grow larger, they tend to spend more time selectively picking aquatic invertebrates from the bottom. Trout over 25 cm TL are active pursuers of large prey, especially other fish (including their own young) and active invertebrates such as crayfish and dragonfly larvae. There are, of course, many exceptions to this general description. In particular, trout of all sizes are prone to feeding on drift during the late summer when the populations of large aquatic insect larvae are reduced. They also feed on emerging aquatic insects when a large hatch is taking place. Most terrestrial insects are taken during the day, although feeding activity (mostly on aquatic organisms) is most intense at dawn and dusk. Active feeding, however, can be observed at nearly any time (Chaston, 1969). In lakes, small brown trout feed heavily on zooplankton, gradually switching first to bottom-dwelling insect larvae (especially chironomid midge larvae) and amphipods, and then (at sizes greater than 25 to 35 cm TL) to fish.

Growth in brown trout is as variable as the waters they inhabit. In California, they reach anywhere from 3 to 8 cm TL (usually 5 to 7 cm TL) in the first year; 7 to 22 cm TL (usually 13 to 16 cm TL) in their second; 13 to 36 cm TL (usually 19 to 28 cm TL) in their third, and 23 to 45 cm TL (usually 35 to 41 cm TL) in their fourth (Carlander, 1969). Brown trout can reach large sizes: the largest known is a 103 cm TL (18 kg) sea-run individual from Scotland, while the largest recorded from California was a 10.9 kg fish from Regulator Lake (Anonymous, 1964). They can live as long as eighteen years, but the oldest known from California was only nine years old, from Castle Lake. Growth is usually faster in lakes than streams but this does not seem to apply to high alpine situations, where growth is poor in both habitats. Growth is affected by temperature, alkalinity, total dissolved solids, turbidity, population density, and food availability.

Brown trout usually become mature in their second or third year, although a few may wait as long as seven or eight years. Spawning takes place in the fall or winter, commonly in November and December in California. Most brown trout populations require streams with gravel riffles that have pea- to walnut-sized gravel for spawning. The most suitable locations are at the tails of pools, where the water is deeper, the current less turbulent, and cover close by. In some large lakes, successful spawning will occasionally take place on gravel bars close to shore.

The reproductive cycle and spawning behavior of brown trout is described and pictured in detail by Frost and Brown (1967). The initial stimulus for upstream movement to the spawning grounds is often a rise in water level, although selection of the spawning site does not occur until water temperatures have dropped to 6 to 10°C. The redd site is selected by the female and she soon starts a depression by turning on her side and digging with her tail (termed "cutting"). The gravel is moved downstream by the suction created by the upward movement of the tail and by the stream current. The initial cutting attracts a male, who defends the female and redd from other males. The male does not help with the construction of the redd but continually courts the female as she works. Courtship consists of swimming alongside the female and quivering. As the redd becomes deeper, courting becomes more intense. Finally the female sinks into the depression, with her anal fin resting on the bottom, and opens her mouth. The male immediately swims alongside her, quivering violently, mouth open, and releases his sperm as the female releases her eggs. The sperm is frequently visible to the observer for a few seconds as a white cloud on the bottom of the nest.

Following the spawning act, the female begins cutting again above the redd, simultaneously burying the newly fertilized eggs and digging a new redd. The spawning act must be repeated several times since each female normally lays only 100 to 250 eggs in each cut. Each female lays a total of 200 to 21,000 eggs, the number depending in part on her size (about 30 to 40 eggs pe cm of FL).

The eggs hatch in four to twenty-one weeks, typically seven to eight weeks, depending on watei temperature. The alevins emerge from the gravel and begin feeding three to six weeks later. The fry tend to live in the quiet waters close to shore, among large rocks or under overhanging plants.

Brown trout occasionally hybridize with brook trout, and the sterile offspring are known as tiger trout, after the distinctive banding on their sides.

Status. Brown trout are abundant in over 5,000 km of California streams and in numerous lakes (Staley, 1966). Their presence in the state is a mixed blessing. On the positive side, they provide some of the finest wild-trout angling in California. Their bottom feeding and piscivorous tendencies, coupled with their natural wariness, make them extremely difficult for the inexperienced angler to catch. Thus they can maintain substantial populations of large fish even in heavily fished streams that receive regular plants of rainbow trout. For the experienced angler they can provide much pleasure, if he can just keep the hatchery rainbows off his hook! A number of streams in California (e.g., Hat Creek, Owens River) are now being managed as wild brown trout streams.

On the other hand, brown trout often have a decidedly negative effect on the populations of other fishes, including other trout. In lakes and stream pools, the production of wild, catchable size trout of all species can sometimes be increased considerably by removing large brown trout that subsist mostly on the other fish. Competition and predation from brown trout may be one factor that has contributed to the decline of the Dolly Varden in the McCloud River. They may also have reduced populations of the rare Modoc sucker in Rush Creek, Modoc County, since there is a strong negative correlation between brown trout abundance and Modoc sucker abundance in the stream (Moyle and Marciochi, in press).

APPENDIX 3 STUDY AREA

The following description is excerpted from a draft of Studley et al. (1995).

Three streams were selected for the Altered Flows Project: the North Fork Middle Fork Tule River (NFMFTR), Tulare County, California; and South Fork Willow Creek (SFWC) and North Fork Willow Creek (NFWC), Madera County, California. These streams are part of PG&E's Tule River (FERC 1333) and Crane Valley (FERC 1354) hydroelectric projects. These streams were selected as the most feasible locations to collect long-term fish population data under two different flow regimes due to the relicensing of the two hydroelectric projects.

Each stream is stratified into homogeneous stream segments which are based on physical, morphological, and hydrologic characteristics. Each stream segment is represented by two or more fish population monitoring study sites (electrofishing stations), except NFMFTR above Tule River Diversion Dam which has only one study site. Long-term fish population data (1984-to date), historic flow data, stream temperature data, and habitat mapping data are available.

TULE RIVER PROJECT STUDY AREA

The Tule River Project consists of three diversion dams, a pumping station, conduit, penstock, a two-unit powerhouse, two transmission lines, and minor features such as access roads. The project was constructed between 1903-1914 by San Joaquin Power and Light. PG&E assumed control of the project through a series of mergers in the 1930's. The project is a run-of-the-river project and diverts up to 66 cfs from the NFMFTR at the Tule River Diversion Dam at an elevation 4000 ft. The project has a 6.4 MW normal operating capacity and average annual generation of 28.4 GWh. Doyle Springs Housing Development (a development of 50 cabins used mainly in the summer) and Wishon Campground (a 36-unit, USFS-run campground) are the only local developments in addition to PG&E's hydroelectric project facilities. The drainage area of the project is 34.7 square miles. Median monthly flows above the diversion dam reach a high of 120 cfs in May and a low of 12 cfs in September. Maximum flows have exceeded 2,000 cfs in 8 years during 1950-1984, and reached 16,900 cfs in December 1966.

Electrofishing stations for the Altered Flows Project were selected in four stream segments at the Tule River Project: NFMFTR above Tule River Diversion Dam, NFMFTR below Tule River Diversion Dam, NFMFTR below Doyle Springs Diversion Dam, and NFMFTR below Meadow Creek. The description for the segment we are currently focusing on is included here (= Segment 8).

NFMFTR BELOW TULE RIVER DIVERSION DAM

The stream segment below Tule River Diversion Dam is approximately 1.1 km long, extending from Tule River Diversion Dam to Doyle Springs Diversion Dam. The elevations of this stream segment range from 3800-4000 ft. Instream flows in this stream segment are partially controlled by the Tule River Diversion Dam which has a capacity of 66 cfs. PG&E voluntarily released approximately 1.5 cfs at the Tule River Diversion Dam until 1994. Natural flows above 66 cfs spill at the Tule River Diversion Dam. Fifty percent exceedance flows range from 1.1 cfs in January to 62.1 cfs in May. Median monthly stream flows have only ranged up to 13.8 cfs during the current California drought (1987-1991), although a high mean hourly flow of greater than 1000 cfs occurred on March 4, 1991.

NFMFTR below Tule River Diversion Dam is represented by two 100-m electrofishing stations. Data have been collected at these stations since fall 1986. An IFIM study was conducted in 1989 using transects located in both electrofishing stations. Macrohabitats in this stream segment consist primaril of pools and pocket water. Mean width and depth at 1.1 cfs is 4.6 m and 31.6 cm, respectively. Mean maximum pool depth is 95.8 cm. Cobble and rubble are the dominant substrates. Cover is provided for about 11.5 percent of the area. Approximately 2 percent of the wetted area is spawning habitat.

Fish species present include wild rainbow and brown trout, and hatchery rainbow trout. Rainbow trou are dominant in terms of numbers but brown trout are dominant in terms of biomass. The majority of hatchery rainbow trout disappear within a week of being planted and they are not known to survive through the winter. The California Department of Fish and Game plants approximately 10,000 rainbow trout per year between April and September (most of them in the vicinity of Wishon Campground but outside of our electrofishing stations). Wild rainbow trout spawn successfully every year but brown trout redds and fry life stages are often subjected to high flows in winter months that essentially eliminate whole year classes. Brown trout year classes were essentially eliminated in this stream segment in 1986 and 1991. Stream temperatures are similar, but slightly warmer, than the stream segment above Tule River Diversion Dam and are not considered limiting to trout.

APPENDIX 4 MATHCAD FILES

A MathCad worksheet is a small computer program created using the software Mathcad 4.0 (MathSoft Inc., Cambridge, MA). These worksheets have been included as an appendix because they are an invaluable link between the description of the model, the computer code, and interpretation of results from simulations. They provide a quick means of checking that the values produced by an equation are realistic (e.g., fecundity or swim speeds agree with values from the literature). Each worksheet, because it is a computer program, provides a means of evaluating the effect of changing a parameter value or functional form prior to making the same change in the simulation model. The worksheets are ordered by their equation in the report; the first line of each worksheet gives the equation number. The parameter and variable names used in the report are also used in these worksheets in most cases. The parameter values used in these worksheets are generally the same as those in Appendix 1. Those equations in Sections 3–8 of this report for which MathCad worksheets are included in this appendix are listed below.

3. Spawning
    - Eq. 3-2. Fecundity = f(length of female)
4. Development and Mortality in the Redd
    - Eq. 4-2. Development rate = f(temp)
    - Eq. 4-3. Probability of scouring = f(water velocity)
5. Growth: Foraging and Consumption
    - Eqs. 5-2 & 5-3. Reactive distance
    - Eqs. 5-9 & 5-10. Maximum and optimum swim speed
    - Eq. 5-14. Temperature dependence of Cmax
    - Eq. 5-14. Cmax = f(weight, temperature)
6. Growth: Energetic Costs
    - Eqs. 6-2 & 6-3. Egestion and Excretion = f(temperature and proportion of Cmax).
    - Eq. 6-5. Standard respiration = f(weight, temperature)
    - Eq. 6-5. Activity respiration = f(temperature, velocity)
    - Eqs. 6-5 & 5-13. Temperature functions for Rstd and Cmax
    - Eq. 6-6. Weight = f(length)
8. Mortality
    - Eqs. 8-1 & 8-2. Pmort = f(condition factor, length)
    - Eq. 8-4. Pfish = f(density of trout)

Filename: FECUNDIT.MCD **Version: August 9, 1995** **Equation 3-2**

The purpose of this worksheet is to illustrate our equation for number of mature ova (F) in the ovaries of a female at the time of spawning as a function of the length (L) of the female on the day of spawning. Values for the two parameters are not specific to the Tule River. These values are based on data for brown trout in streams in Wisconsin (Avery 1985). We use the same values for brown and rainbow trout.

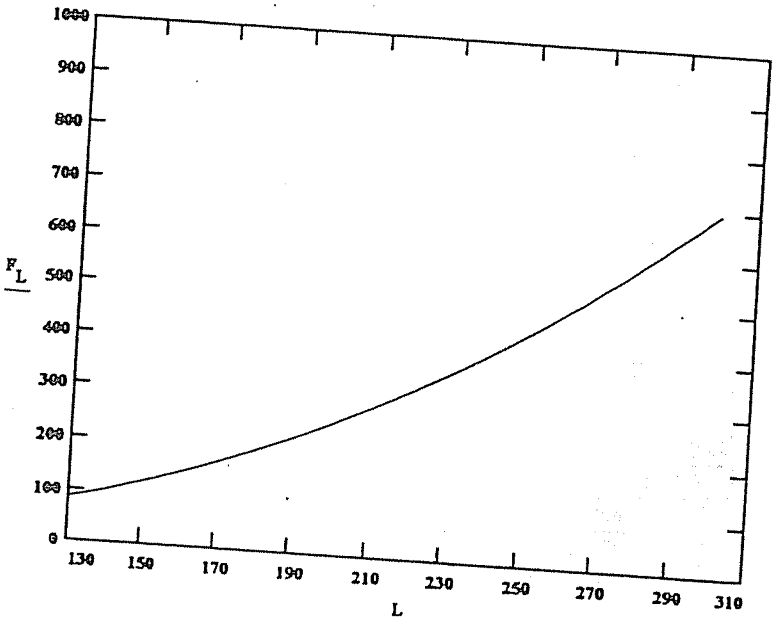
$a := 1.16$ $b := 2.54$ $L := 130, 135..300$ **(Fork length, mm)** $Lin_L := 1.05 \cdot \frac{L}{25.4}$ **(Total length, in)**

$F_L := a \cdot \left(Lin_L\right)^b$ **Fecundity**

The minimum fork length for sexual maturity of a female is 130 mm for RT and 170 mm for BT.

The value of the parameter b of 2.54 means that the number of mature eggs increases faster than the length of the female trout, but not faster than her weight (assuming W is proportional to L3). Values for the a and b parameters above are from Avery's (1985) regression equation with length as total length of the trout in inches--thus the conversion of L values to Lin values.**

Lin_L	L	F_L
5.4	130	83
5.6	135	91
5.8	140	100
6	145	110
6.2	150	119
6.4	155	130
6.6	160	141
6.8	165	152
7	170	164
7.2	175	177
7.4	180	190
7.6	185	204
7.9	190	218
8.1	195	233
8.3	200	248
8.5	205	264
8.7	210	281
8.9	215	298
9.1	220	316
9.3	225	335
9.5	230	354
9.7	235	374
9.9	240	394
10.1	245	415
10.3	250	437
10.5	255	460
10.7	260	483
11	265	507
11.2	270	532
11.4	275	557
11.6	280	583
11.8	285	610
12	290	638
12.2	295	666
12.4	300	695



Fork length, mm

Filename: DEVRATE.MCD Version: August 9, 1995 Equation 4-2

The purpose of this worksheet is to illustrate our equation for the daily rate of development (R, 1/day) as a function of temperature (T, oC) from fertilization of the eggs spawned by a female to 50% emergence of the surviving alevins, which we then call fry and follow as individual fish. Day of emergence is a function of the temperature regime between spawning and emergence. Day of 50% emergence is determined by accumulating daily values for R until the day the cumulative sum equals or exceeds 1.0. We assume that the fractional development that takes place on any given day at temperature T is equivalent to the reciprocal of the number of days from fertilization to 50% emergence if the temperature were held constant at that value.

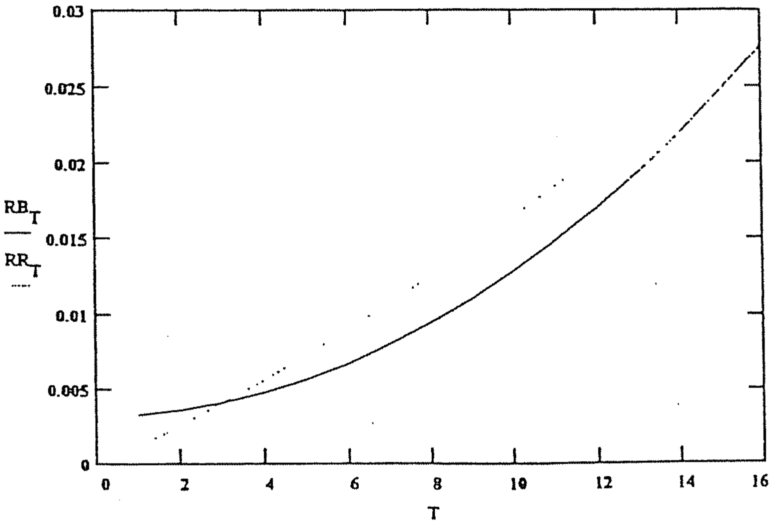
Parameter values given below were estimated separately for the two species by fitting a quadratic regression equation to Embody's (1934) data (after extrapolation) on number of days to 50% hatch of eggs at various constant temperatures for brown and rainbow trout. The extrapolation step involves using data from Elliott (1984a) on brown trout to extrapolate Embody's data from 50% hatch of eggs to 50% emergence of fry. The regression model is T.0/(1,2..16 50% emergence) = R = a + b*T + c*T*T.

Brown Trout: $aB := 0.00313$ $bB := 0.0000307$ $cB := 0.0000934$ $RB_T = aB + bB \cdot T + cB \cdot T^2$ $DB_T := \frac{1}{RB_T}$

Rainbow Trout: $aR := -0.000254$ $bR := 0.00134$ $cR := 0.0000321$ $RR_T := aR + bR \cdot T + cR \cdot T^2$ $DR_T = \frac{1}{RR_T}$

RB and RR values are daily development rates (1/days) for brown (B) and rainbow (R) trout, respectively. DB and DR are days from fertilization to 50% emergence. Note that there are substantial differences between the two species. Rainbow trout have a much faster rate of development than brown trout, except at low temperatures.

T	RB_T	RR_T	DB_T	DR_T
1	0.0033	0.0011	307	894
2	0.0036	0.0026	281	391
3	0.0041	0.0041	246	247
4	0.0047	0.0056	211	178
5	0.0056	0.0072	178	138
6	0.0067	0.0089	150	112
7	0.0079	0.0107	126	93
8	0.0094	0.0125	107	80
9	0.011	0.0144	91	69
10	0.0128	0.0164	78	61
11	0.0148	0.0184	68	54
12	0.0169	0.0204	59	49
13	0.0193	0.0226	52	44
14	0.0219	0.0248	46	40
15	0.0246	0.0271	41	37
16	0.0275	0.0294	36	34



Filename: PSCOUR.MCD **Version: Sep 25, 1995** **Equation 4-3**

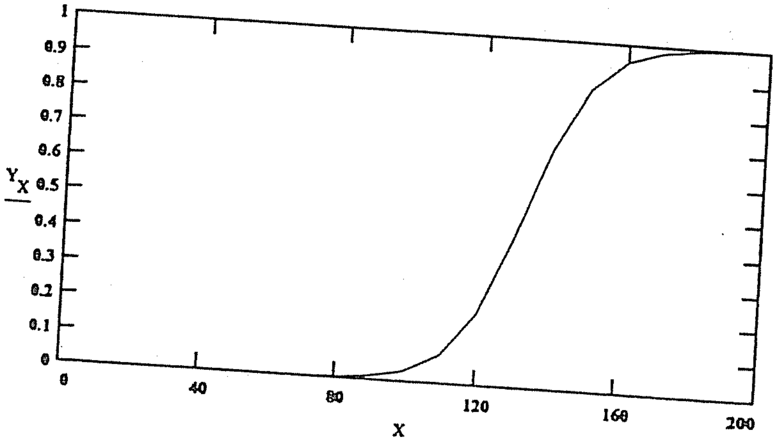
The purpose of this worksheet is to evaluate our function for the daily risk of mortality to eggs and alevins in a redd due to scouring (Pscour) as a function of the average water column velocity (Vave) in the cell in which the model redd is located. Our equation for Pscour is an increasing logistic function of Vave. In what follows below, X = Vave and has units of cm/s rather than m/s because X as a subscript in Mathcad is required to be an integer, and Y = Pscour. We require that this function pass through the two points (X1, Y1) and (X2, Y2). These two points are selected based on a combination of empicial data and expert judgement. We use the first half of the algorithm developed by Thornten and Lessem (1978) for parameterizing a logistic function. In this case we use their first two equations which fit an increasing logistic function through two points, one fairly close to Y = 0.0 and the second close to Y = 1.0.

$X := 0, 10 .. 200$ $\quad X1 := 90$ $\quad X2 := 160$ $\quad$ (cm/sec)

$Y1 := 0.01$ $\quad Y2 := 0.95$

$$A_X := \frac{1.0}{X2 - X1} \cdot \ln\left[\frac{Y2 \cdot (1.0 - Y1)}{Y1 \cdot (1.0 - Y2)}\right] \qquad Y_X := \frac{Y1 \cdot \exp\left[A_X \cdot (X - X1)\right]}{1.0 + Y1 \cdot \left[\exp\left[A_X \cdot (X - X1)\right] - 1.0\right]}$$

X	Y_X
0	$6.23 \cdot 10^{-7}$
10	$1.83 \cdot 10^{-6}$
20	$5.37 \cdot 10^{-6}$
30	$1.58 \cdot 10^{-5}$
40	$4.63 \cdot 10^{-5}$
50	$1.36 \cdot 10^{-4}$
60	$3.99 \cdot 10^{-4}$
70	0
80	0
90	0.01
100	0.03
110	0.08
120	0.2
130	0.43
140	0.69
150	0.87
160	0.95
170	0.98
180	0.99
190	1
200	1



X is average water column velocity in cm/s

Filename: RD.MCD Version: August 9, 1995 Equations 5-2 and 5-3

Reactive distance is the distance between a trout and a prey item at which the trout reacts to having seen the prey item by initiating a strike. Reactive distance for drift foragers decreases as velocity (Vf, cm/s) increases (Godin and Rangeley 1989; Grant and Noakes 1987; Hill and Grossman 1993; Hughes and Dill 1990) and increases with temperature (T) and length (L, cm) of the trout. We used empirical data from experiments by Hill and Grossman (1993) and logistic regression to develop a model for the probability of capture (Pcap) as a logistic function of these three variables and the distance between the prey and the trout (PD, in units of body lengths rather than cm). We use the ratio of water velocity to trout length as a
variable that reflects the relative water velocity in body lengths/second.
Our equation is:

Pcap = exp(Y)/[1.0 + exp(Y)] , where (5-2)
Y = aRD + bRD Vf/L + cRD T + dRD PD .

To convert this expression into a model for reactive distance (RD), we define RD (in units of body lengths at this point) as the distance between trout and prey that results in a 90% probability of
capture (Pcap = 0.9) and solve Equation (5-2) for RD (in place of PD):

RD = {ln[0.9/(1-0.9)] - aRD - bRD Vf/L - cRD T} L/dRD ,0 <= RD <= RDmax ,(5-3)
= 0 , RD < 0 ,
= RDmax , RD > RDmax ,

where RDmax is the maximum reactive distance in body lengths. We use this equation for both drift and benthic feeding.

$L := 2..30$ (cm) $V := 0..50$ (cm/s) $T := 1..25$ (oC) $RDmax := 100$ (cm)

$Pcap := 0.9$ $ard := -5.91$ $brd := 0.847$ $crd := -0.0473$ $drd := 1.74$

$$Pcap = \frac{\exp\left(ard + brd\cdot\frac{V}{L} + crd\cdot T + drd\cdot RD\right)}{1.0 + \exp\left(ard + brd\cdot\frac{V}{L} + crd\cdot T + drd\cdot RD\right)}$$

Use Mathcad's symbolic processor to solve this equation for RD. The result is given below.

$$\frac{\left[\ln\left[-1.\cdot\frac{Pcap}{(Pcap-1.)}\right] - 1.\cdot ard - 1.\cdot brd\cdot\frac{V}{L} - 1.\cdot crd\cdot T\right]}{drd}$$

$$RD(V,L,T) := \frac{\left[\ln\left[-1.\cdot\frac{Pcap}{(Pcap-1.)}\right] - 1.\cdot ard - 1.\cdot brd\cdot\frac{V}{L} - 1.\cdot crd\cdot T\right]}{drd}$$

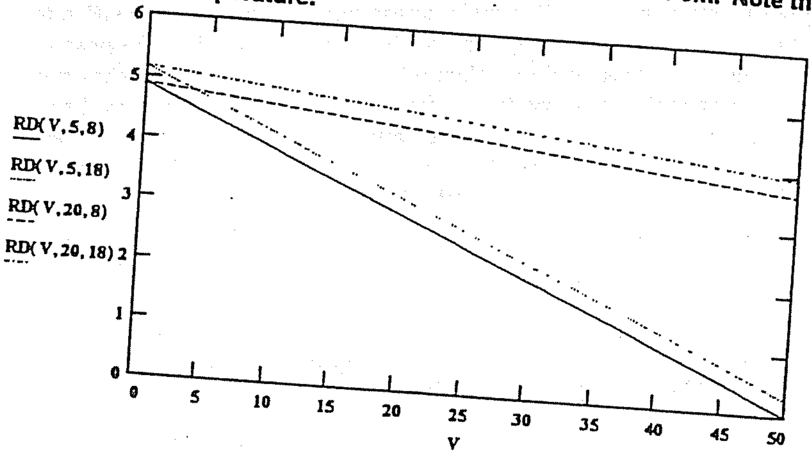
$RD(V,L,T) := if(RD(V,L,T)>RDmax, RDmax, RD(V,L,T))$

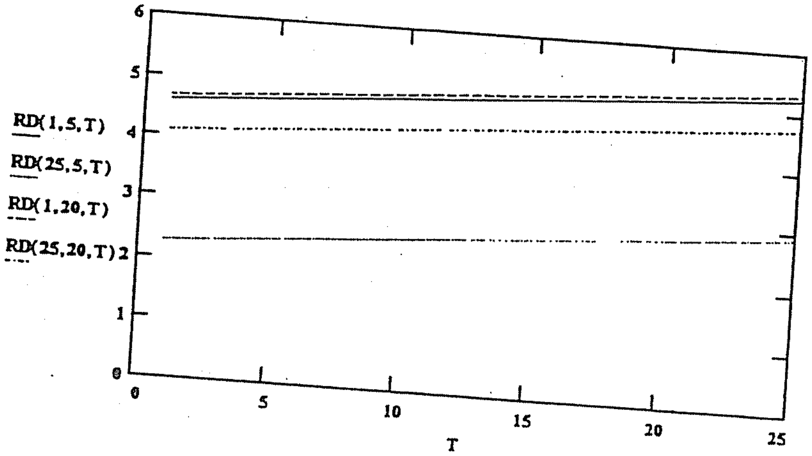
$RD(V,L,T) := if(RD(V,L,T)<0, 0, RD(V,L,T))$

Note that the values for the parameters "ard" and "crd" are negative. In combination with the minus signs in the equation for RD for these two tterms, this equation is equivalent to Eq. (5-3) in the text, which has plus signs for these two terms.

Equations 5-2 and 5-3, continued. Page 2.

The graphs below illustrate (1) reactive distance (RD) as a function of velocity for two lengths of trout (5 and 20 cm) at two temperatures (8 and 18 C); and (2) RD as a function of temperature at two velocities (1 and 25 cm/s) and two lengths of trout (5 and 20 cm). All values of RD have units of body lengths. In the simulation model, RD has units of cm. Note that RD varies more with velocity than temperature.





Filename: SWIM.MCD **Version: August 9, 1995** **Equations 5-9 and 5-10**

This worksheet illustrates the equations for optimum swim speed and maximum swim speed. In both cases, swim speed is a function of the size of the trout (W, g wet weight, which is calculated from the trout's length (L) using the allometric equation for BT or RT) and the temperature (T) on that day. The optimum swim speed is that swim speed which maximizes growth rate. Parameter values are estimated separately for trout less than or equal to 150 grams wet weight and trout more than 150 grams wet weight. Maximum swim speed is the maximum swim speed a fish can sustain for a specified time, typically one hour; parameter values are based on Stewart (1980, p. 46). The two equations have the same form; all that differs are the parameter values. Parameter values are the same for BT and RT. For this worksheet we use RT parameters to go from length of a trout to its weight (g wet wt).

$L := 2..30$ **(cm)** $T := 1..25$ **(oC)**

Rainbow trout$aL := 0.0000147$ $bL := 2.96$ $W(L) = aL\cdot(10\cdot L)^{bL}$

The length of a trout having the threshold weight of 150 g is 23.35 cm, i.e.,

$W(23.35) = 150$

Optimum swim speed (cm/s). The parameter values for dswim and eswim change at a wet weight of 150 grams.

$dswim(L) := 9.70\cdot(W(L)>150) + 2.84\cdot(W(L)\le 150)$

$eswim(L) := 0.128\cdot(W(L)>150) + 0.485\cdot(W(L)\le 150)$

$fswim := 0.0405$

$Sopt(L,T) := dswim(L)\cdot W(L)^{eswim(L)}\cdot \exp(fswim\cdot T)$

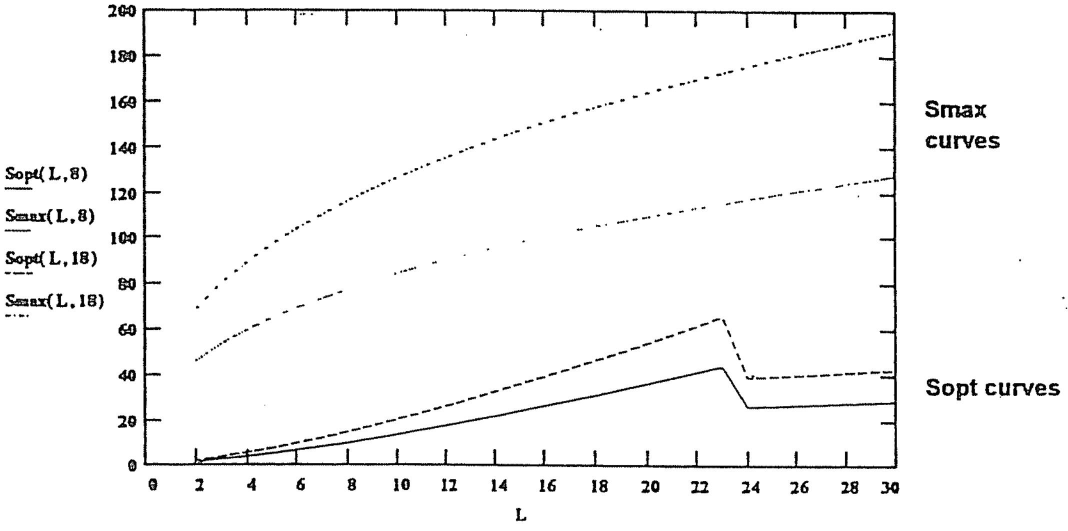
Maximum swim speed (cm/s)

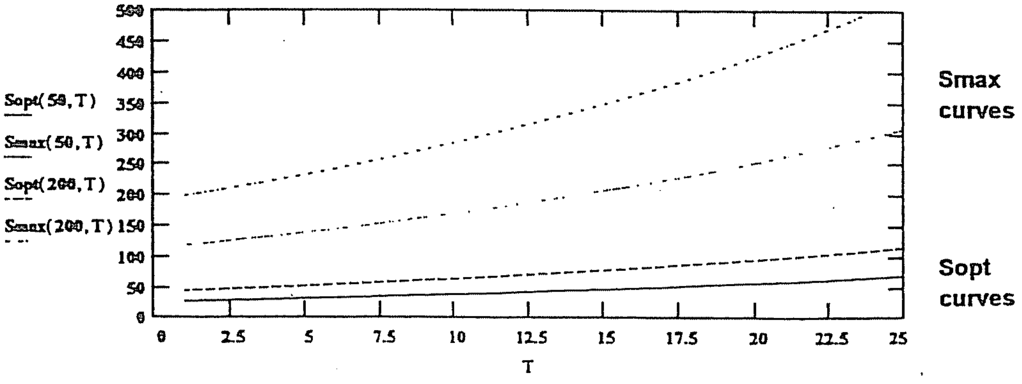
$aswim := 44.1$

$bswim := 0.128$

$cswim := 0.0405$

$Smax(L,T) := aswim\cdot W(L)^{bswim}\cdot \exp(cswim\cdot T)$

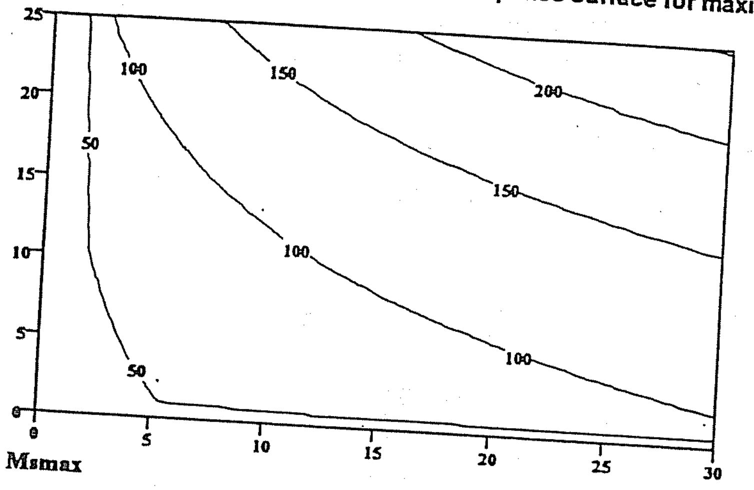




Equations 5-9 and 5-10, continued. Page 2. All contours for swimming speed on this page have units of cm/s

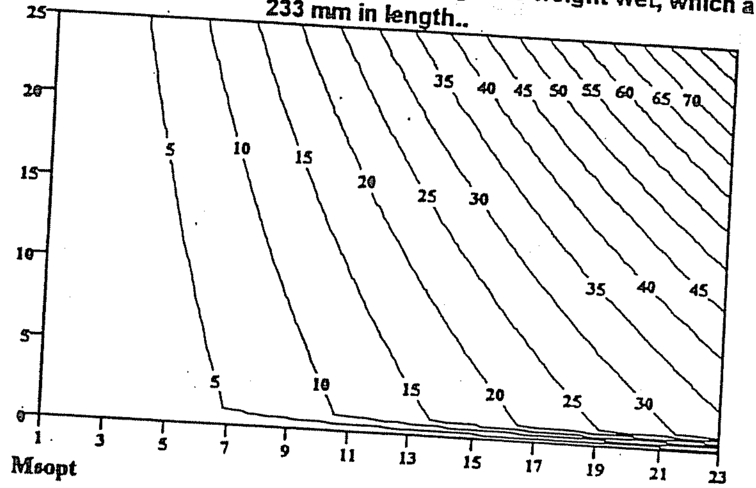
$i := 2..30$ $j := 1..25$ $L_i := i$ (cm) $T_j := j$ (oC)

$Msmax_{i,j} := Smax(L_i, T_j)$ **This is the (L,T) response surface for maximum swim speed**



$i := 2..23$ $L_i := i$ $j := 1..25$ $T_j := j$ $Sopt(L,T) := 2.84 \cdot W(L)^{0.485} \cdot \exp(fswim \cdot T)$

$Msopt_{i,j} := Sopt(L_i, T_j)$ **This is the (L,T) response surface for optimum swim speed for trout weighing <= 150 grams weight wet, which applies for trout from 20 to 233 mm in length..**



Filename: CMAXT.MCD Version: August 10, 1995 Equation 5-14

The purpose of this worksheet is to compare the temperature multiplier, FT, for maximum consumption (Cmax) for brown and rainbow trout. A "B" at the end of a variable or parameter name denotes brown trout; a "R" at the end of a variable or parameter name denotes rainbow trout. The function FT requires values for 8 parameters, i.e.,the (T, FT) coordinates for four points through which we want the curve to pass.

$T := 0, 1 .. 25$

$T1B := 7.0 \quad T2B := 15.0 \quad T3B := 18.0 \quad T4B := 21.0$ Current parameter estimates

$F1B := 0.20 \quad F2B := 0.70 \quad F3B := 0.98 \quad F4B := 0.20$

$$A(T, T1B, T2B, F1B, F2B) := \frac{1.0}{T2B - T1B} \cdot \ln\left[\frac{F2B \cdot (1.0 - F1B)}{F1B \cdot (1.0 - F2B)}\right]$$

$$KAB(T, T1B, T2B, F1B, F2B) := \frac{F1B \cdot \exp(A(T, T1B, T2B, F1B, F2B) \cdot (T - T1B))}{1.0 + F1B \cdot (\exp(A(T, T1B, T2B, F1B, F2B) \cdot (T - T1B)) - 1.0)}$$

$$B(T, T3B, T4B, F3B, F4B) := \frac{1.0}{T4B - T3B} \cdot \ln\left[\frac{F3B \cdot (1.0 - F4B)}{F4B \cdot (1.0 - F3B)}\right]$$

$$KBB(T, T3B, T4B, F3B, F4B) := \frac{F4B \cdot \exp(B(T, T3B, T4B, F3B, F4B) \cdot (T4B - T))}{1.0 + F4B \cdot (\exp(B(T, T3B, T4B, F3B, F4B) \cdot (T4B - T)) - 1.0)}$$

$$FB(T, T1B, T2B, T3B, T4B, F1B, F2B, F3B, F4B) := KAB(T, T1B, T2B, F1B, F2B) \cdot KBB(T, T3B, T4B, F3B, F4B)$$

The seven "observed" data points (i.e., the arrays of TB and FB1 values below) for brown trout are calculated from data in Table 1 in Elliott (1975c)

$$TB := \begin{bmatrix} 3.8 \\ 5.6 \\ 12.8 \\ 15.0 \\ 17.8 \\ 19.5 \\ 21.7 \end{bmatrix} \quad FB1 := \begin{bmatrix} 0.05 \\ 0.12 \\ 0.59 \\ 0.75 \\ 1.00 \\ 0.30 \\ 0.07 \end{bmatrix}$$

These are the (T,FT) data to which we are fitting the Thornton & Lessem model for brown trout.

$FB(3.8, T1B, T2B, T3B, T4B, F1B, F2B, F3B, F4B) = 0.09$

$FB(5.6, T1B, T2B, T3B, T4B, F1B, F2B, F3B, F4B) = 0.14$

$FB(12.8, T1B, T2B, T3B, T4B, F1B, F2B, F3B, F4B) = 0.56$

$FB(15.0, T1B, T2B, T3B, T4B, F1B, F2B, F3B, F4B) = 0.7$

$FB(17.8, T1B, T2B, T3B, T4B, F1B, F2B, F3B, F4B) = 0.82$

$FB(19.5, T1B, T2B, T3B, T4B, F1B, F2B, F3B, F4B) = 0.69$

$FB(21.7, T1B, T2B, T3B, T4B, F1B, F2B, F3B, F4B) = 0.06$

Table comparing observed and predicted values of the temperature multiplier of Cmax for brown trout. Also the absolute deviation and the sum of these deviations:

Temp	3.8	5.6	12.8	15.0	17.8	19.5	21.7
Observed	0.05	0.12	0.59	0.75	1.00	0.30	0.07
Predicted	0.09	0.14	0.56	0.70	0.82	0.69	0.06
Absol. error	0.04	0.02	0.03	0.05	0.18	0.39	0.01
Sum:	0.72						

Equation 5-14; continued. Page 2. Now for rainbow trout.

$T1R := 4.0$ $T2R := 15.0$ $T3R := 22.0$ $T4R := 24.0$ **Current estimates**

$F1R := 0.20$ $F2R := 0.7$ $F3R := 0.98$ $F4R := 0.20$

$$A(T,T1R,T2R,F1R,F2R) := \frac{1.0}{T2R - T1R} \cdot \ln\left[\frac{F2R \cdot (1.0 - F1R)}{F1R \cdot (1.0 - F2R)}\right]$$

$$KAR(T,T1R,T2R,F1R,F2R) := \frac{F1R \cdot \exp(A(T,T1R,T2R,F1R,F2R) \cdot (T - T1R))}{1.0 + F1R \cdot (\exp(A(T,T1R,T2R,F1R,F2R) \cdot (T - T1R)) - 1.0)}$$

$$B(T,T3R,T4R,F3R,F4R) := \frac{1.0}{T4R - T3R} \cdot \ln\left[\frac{F3R \cdot (1.0 - F4R)}{F4R \cdot (1.0 - F3R)}\right]$$

$$KBR(T,T3R,T4R,F3R,F4R) := \frac{F4R \cdot \exp(B(T,T3R,T4R,F3R,F4R) \cdot (T4R - T))}{1.0 + F4R \cdot (\exp(B(T,T3R,T4R,F3R,F4R) \cdot (T4R - T)) - 1.0)}$$

$$FR(T,T1R,T2R,T3R,T4R,F1R,F2R,F3R,F4R) := KAR(T,T1R,T2R,F1R,F2R) \cdot KBR(T,T3R,T4R,F3R,F4R)$$

The six "observed" data points below for rainbow trout were calculated by Peter Rand (personal communication) from data in Appendix I of From and Rasmussen (1984).

$$TR := \begin{bmatrix} 5.0 \\ 10.0 \\ 15.0 \\ 20.0 \\ 22.0 \\ 24.3 \end{bmatrix} \qquad FR1 := \begin{bmatrix} 0.27 \\ 0.53 \\ 0.68 \\ 0.91 \\ 1.00 \\ 0.18 \end{bmatrix}$$

$FR(5.0,T1R,T2R,T3R,T4R,F1R,F2R,F3R,F4R) = 0.23$

$FB(10.0,T1R,T2R,T3R,T4R,F1R,F2R,F3R,F4R) = 0.46$

$FB(15.0,T1R,T2R,T3R,T4R,F1R,F2R,F3R,F4R) = 0.7$

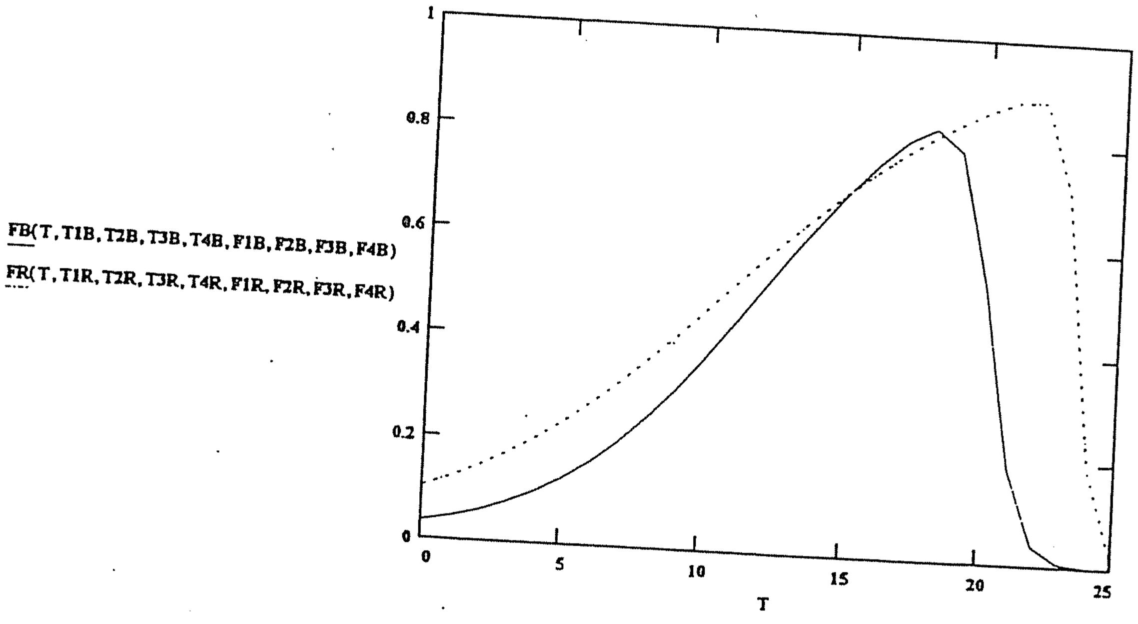
$FB(20.0,T1R,T2R,T3R,T4R,F1R,F2R,F3R,F4R) = 0.87$

$FB(22.0,T1R,T2R,T3R,T4R,F1R,F2R,F3R,F4R) = 0.89$

$FB(24.3,T1R,T2R,T3R,T4R,F1R,F2R,F3R,F4R) = 0.1$

Table comparing observed and predicted values of the temperature multiplier of Cmax for rainbow trout. Also the absolute deviation and the sum of these deviations:

Temp	5.0	10.0	15.0	20.0	22.0	24.3
Observed	0.27	0.53	0.68	0.91	1.00	0.18
Predicted	0.23	0.46	0.70	0.87	0.89	0.10
Absol. error	0.04	0.07	0.02	0.04	0.11	0.08
Sum:	0.36					



Filename: CMAX.MCD   Version:Dec 17, 1995   Equation 5-14

The purpose of this worksheet is to evaluate the weight-dependent function for Cmax and the combined weight- and temperature-dependent formulation for Cmax for BT and for RT.

$L := 2..30$ (cm) $T := 1..25$ (C)

These three columns give parameter values for brown trout.

$ab := 0.0000132 \quad tminb := 7.0 \quad k1b := 0.20$

$bb := 2.97 \quad t2b := 15.0 \quad k2b := 0.70$

$cab := 0.60 \quad t3b := 18.0 \quad k3b := 0.98$

$cbb := -0.24 \quad tmaxb := 21.0 \quad k4b := 0.20$

These three columns give parameter values for rainbow trout.

$ar := 0.0000147 \quad tminr := 4.0 \quad k1r = 0.20$

$br := 2.96 \quad t2r := 15.0 \quad k2r := 0.70$

$car := 0.60 \quad t3r := 22.0 \quad k3r := 0.98$

$cbr := -0.24 \quad tmaxr := 24.0 \quad k4r := 0.20$

Note: the value of cbb = cbr = -0.24 means that the weight-dependent factor in the equation for Cmax is on a weight-specific basis, i.e., grams wet weight of prey consumed per gram wet weight of trout. This scale is useful in evaluating if the formulation for Cmax is giving reasonable values. Expected values for Cmax are in the range of 1% to about 10% (i.e., 0.01 to 0.1 g/g/day), and they tend to be higher for small trout than for large trout.

The following equations for the temperature-dependent factor are algebraically equivalent to the equations in the preceding worksheet CMAXT.MCD on the f(T).

Equations for brown trout

$$kab_T := \left(\frac{k2b}{k1b}\cdot\frac{1-k1b}{1-k2b}\right)^{\frac{T-tminb}{t2b-tminb}}$$

$$kbb_T := \left(\frac{k3b}{k4b}\cdot\frac{1-k4b}{1-k3b}\right)^{\frac{tmaxb-T}{tmaxb-t3b}}$$

$$kab_T := \frac{k1b\cdot kab_T}{1+k1b\cdot\left(kab_T-1\right)}$$

$$kbb_T := \frac{k4b\cdot kbb_T}{1+k4b\cdot\left(kbb_T-1\right)}$$

$$ftb_T := kab_T\cdot kbb_T$$

Equations for rainbow trout

$$kar_T := \left(\frac{k2r}{k1r}\cdot\frac{1-k1r}{1-k2r}\right)^{\frac{T-tminr}{t2r-tminr}}$$

$$kbr_T := \left(\frac{k2r}{k4r}\cdot\frac{1-k4r}{1-k2r}\right)^{\frac{tmaxr-T}{tmaxr-t3r}}$$

$$kar_T := \frac{k1r\cdot kar_T}{1+k1r\cdot\left(kar_T-1\right)}$$

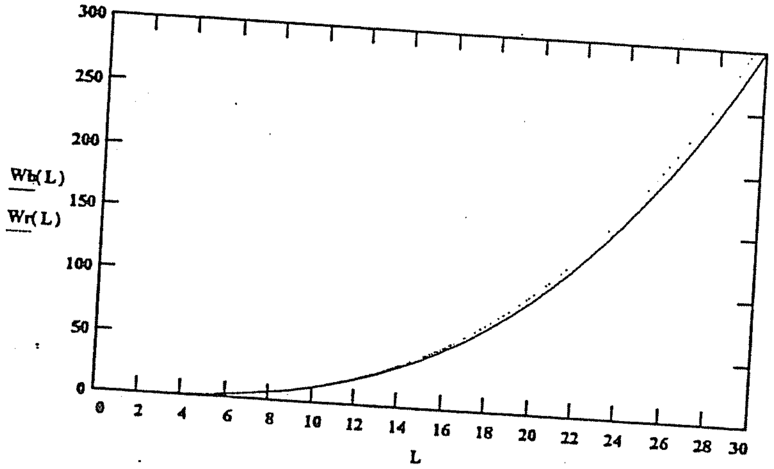
$$kbr_T := \frac{k4r\cdot kbr_T}{1+k4r\cdot\left(kbr_T-1\right)}$$

$$ftr_T := kar_T\cdot kbr_T$$

Equation 5-14 for Cmax, continued. Page 2. On this page we illustrate the curves for the weight of a trout (g wet weigth) as a function of its length (cm), and the curves for weight-specific maximum consumption as a function of length. The temperature factor is assumed to have a value of 1.0, i.e., Cmax as a function of the weight of the trout at the optimum temperature.

$Wb(L) := ab \cdot (10 \cdot L)^{bb}$ (g)

$Wr(L) := ar \cdot (10 \cdot L)^{br}$(g)



We now evaluate the weight-dependent factor in the Cmax function using different values for the intercept parameter, ca. We use the RT parameter values for the W-L equation illustrated

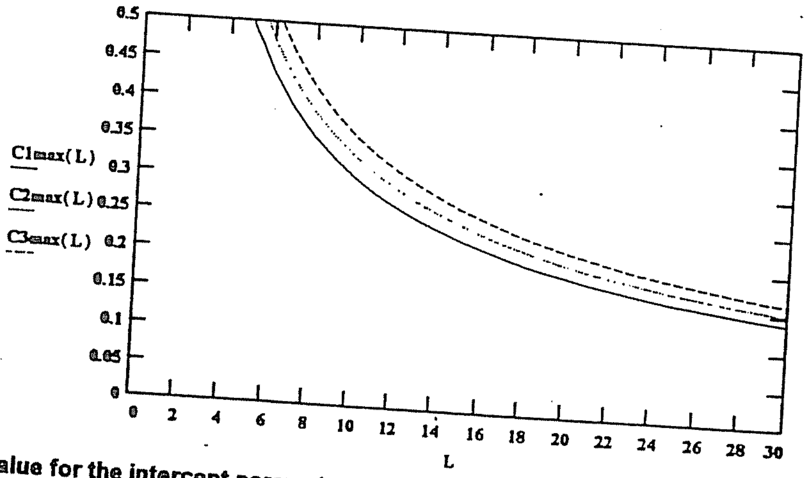
$ca := cab$ $ca := car$ $cb := cbb$ $cb := cbr$ $cb := -0.24$

$ca1 := 0.55$

$ca2 := 0.60$ (0.60 is the baseline value)

$ca3 := 0.65$

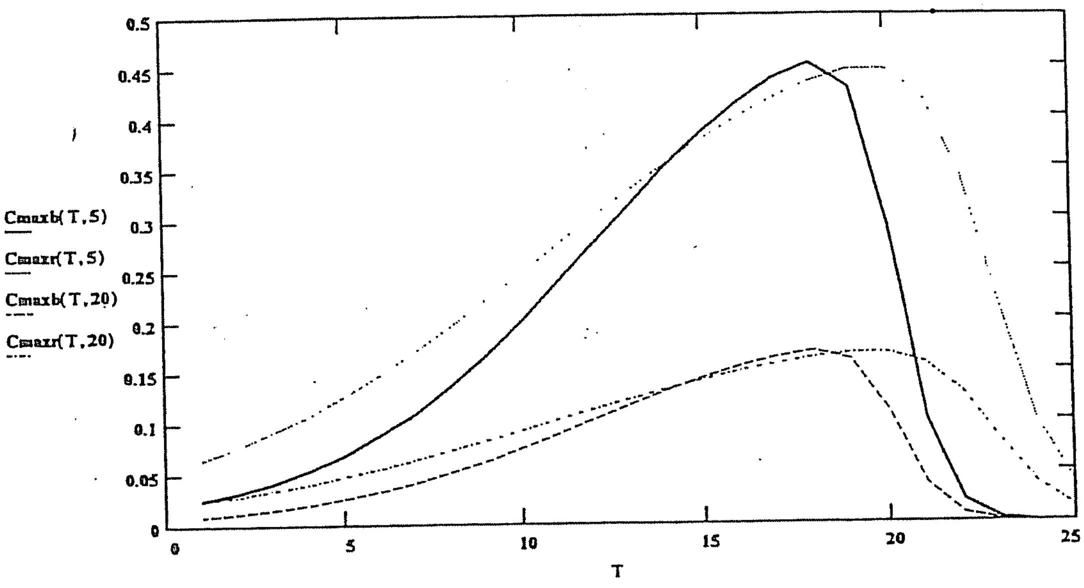
$C1max(L) := ca1 \cdot Wr(L)^{cb}$ $C2max(L) = ca2 \cdot Wr(L)^{cb}$ $C3max(L) := ca3 \cdot Wr(L)^{cb}$



The value for the intercept parameter ca is estimated in calibrating the model for the baseline simulation. Our calibration criterion is that the maximum weight-specific consumption (i.e., grams wet weight of prey consumed per gram wet weight of trout per day) at optimum temperatures is in the range of 10-20% for Age 0 trout and 5-15% for Age 1 and older trout (Elliott 1975b, p.293, Figure 5; Brett and Groves 1979, p. 297, Figure 3).

Equation 5-14 on Cmax, continued. Page 3. On this page we illustrate the dependence of Cmax on the weight of the trout and temperature combined. We do this by fixing the size of the trout by specifying a length in cm (i.e., 5 cm and 20 cm), and then plotting the curve of Cmax vs T for a trout of that length. Two of the curves are for BT (denoted with "b") and two are for RT (denoted with a "r").

$\mathrm{Cmaxb}(T,L) := \left(\mathrm{ca2}\cdot \mathrm{Wb}(L)^{cb}\right)\cdot \mathrm{ftb}$(g/g/d) $\qquad \mathrm{Cmaxr}(T,L) := \left(\mathrm{ca2}\cdot \mathrm{Wr}(L)^{cb}\right)\cdot \mathrm{ftr}$(g/g/d)



Filename: EG&EX.MCD **Version: Nov 12, 1995** **Equations 6-2 and 6-3**

The purpose of this file is to evaluate the formulations in our trout ibm for egestion and excretion. For each of these processes the formulation is a function of temperature (T) and proportion of maximum consumption (P = WEATEN/CMAX). For each of these processes we assume the same parameter values for all trout species.

$N1 := 12$ $\quad i := 2,4..N1$ $\quad T_i := 2 \cdot i$

$N2 := 10$ $\quad j := 0,2..N2$ $\quad P_j := \frac{j}{10.0}$

These equations give the fraction of what is actually consumed that is lost in egestion and excretion. These fractions are independent of the size of the fish. These fractions multiply Cmax, which does dependent on fish size.

$EGA := 0.212$ $\quad EGB := -0.222$ $\quad EGC := 0.631$

$EXA := 0.0314$ $\quad EXB := 0.580$ $\quad EXC := -0.299$

$FA(T,P) := \left(EGA \cdot T^{EGB}\right) \cdot \exp(EGC \cdot P)$ $\quad UA(T,P) := \left(EXA \cdot T^{EXB}\right) \cdot \exp(EXC \cdot P)$

$MFA_{i,j} := FA\left(T_i, P_j\right)$ $\quad MUA_{i,j} := UA\left(T_i, P_j\right)$

The above parameter estimates are from a multliple regression analysis by Elliott (1976b) using his BT data. On the next page we have a contour plot for the response surface of these two functions using additional levels of T and P. The column vectors on this page allow one to confirm calculations and get a feel for the function.

T_i	P_j	$MFA_{i,j}$	$MUA_{i,j}$
4	0	0.156	0.07
8	0.2	0.177	0.066
12	0.4	0.201	0.062
16	0.6	0.228	0.059
20	0.8	0.258	0.055
24	1	0.293	0.052
		0.134	0.105
		0.152	0.099
		0.172	0.093
		0.195	0.088
		0.221	0.083
		0.251	0.078
		0.122	0.133
		0.139	0.125
		0.157	0.118
		0.178	0.111
		0.202	0.104
		0.23	0.098
		0.115	0.157
		0.13	0.148
		0.147	0.139
		0.167	0.131
		0.19	0.123
		0.215	0.116
		0.109	0.178
		0.124	0.168
		0.14	0.158
		0.159	0.149
		0.181	0.14
		0.205	0.132
		0.105	0.198
		0.119	0.187
		0.135	0.176
		0.153	0.166
		0.173	0.156
		0.197	0.147

Here is some help so you can determine the correspondence between an element in this long array and the matrix of T,P values.

— This MUA value of 0.198 is for (T,P) = (24.0 C, 0.0)

— This MUA value of 0.147 is for (T,P) = (24.0, 1.0)

Equations 6-2 and 6-3: continued. Page 2. Now for the response surfaces/contour plots. Temperature (T) is on the X axis, and proportion of Cmax (P) is on the Y axis. The lines for the response surface for egestion (MFA) are contours or isolines for the fraction of energy consumed that is lost in egestion (i.e., feces). The lines for the response surface for excretion (MUA) are contours for the fraction of (energy consumed minus egestion) that is lost in excretory products (e.g., urine, mucus). Notice that the two response surfaces are quite different in shape. However, the differences tend to balance each other such that the fractional energy loss due to these two processes is less variable than the individual processes.

$N1 := 12 \qquad i := 1..N1 \qquad T_i := 2 \cdot i$

$N2 := 10 \qquad j := 0..N2 \qquad P_j := \frac{j}{10.0}$

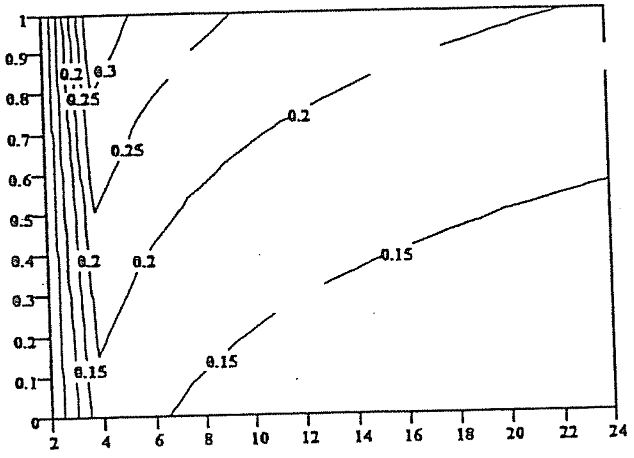
$EGA := 0.212 \qquad EGB := -0.222 \quad EGC := 0.631$

$EXA := 0.0314 \qquad EXB := 0.580 \quad EXC := -0.299$

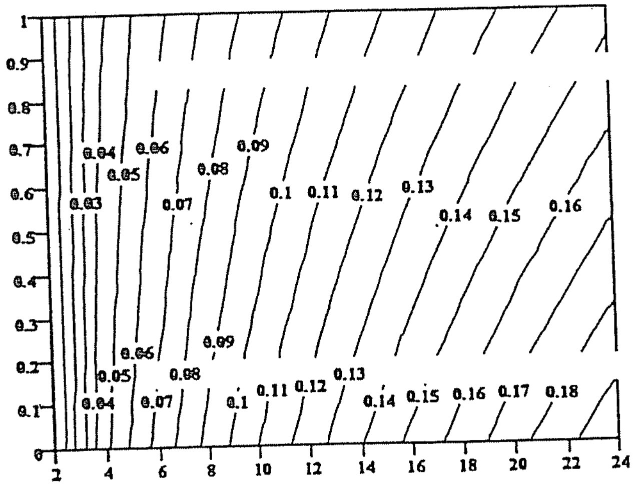
$FA(T,P) := \left(EGA \cdot T^{EGB}\right) \cdot \exp(EGC \cdot P) \quad UA(T,P) := \left(EXA \cdot T^{EXB}\right) \cdot \exp(EXC \cdot P)$

$MFA_{i,j} := FA\left(T_i, P_j\right) \qquad MUA_{i,j} := UA\left(T_i, P_j\right)$

T_i	P_j
2	0
4	0.1
6	0.2
8	0.3
10	0.4
12	0.5
14	0.6
16	0.7
18	0.8
20	0.9
22	1
24	



MFA



MUA

Filename: RESPIRS.MCD **Version: Dec 15, 1995** **Equation 6-5**

The purpose of this worksheet is to evaluate our equation for standard respiration (Rstd, calories/day) as a function of fish weight (W, grams wet weight) and temperature (T, deg C). We use the same parameter values for both species (see Section 6 of this Trout Report). In the contour plot below, temperature is on the X axis and weight of the trout is on the Y axis. Each contour is connecting points of (T,W) resulting in the same daily energetic cost for standard respiration.

$N1 := 12$ $i := 1 .. N1$ $T_i := 2 \cdot i$

$N2 := 30$ $j := 0 .. N2$ $W_j := 10 \cdot j$

Weight (W) has units of grams wet wt

$ar := 7.13$ $br := 0.7836$ $cr := 0.0693$

Weight-to-length equation for RT

$aLr := 0.0000147$ $bLr := 2.96$

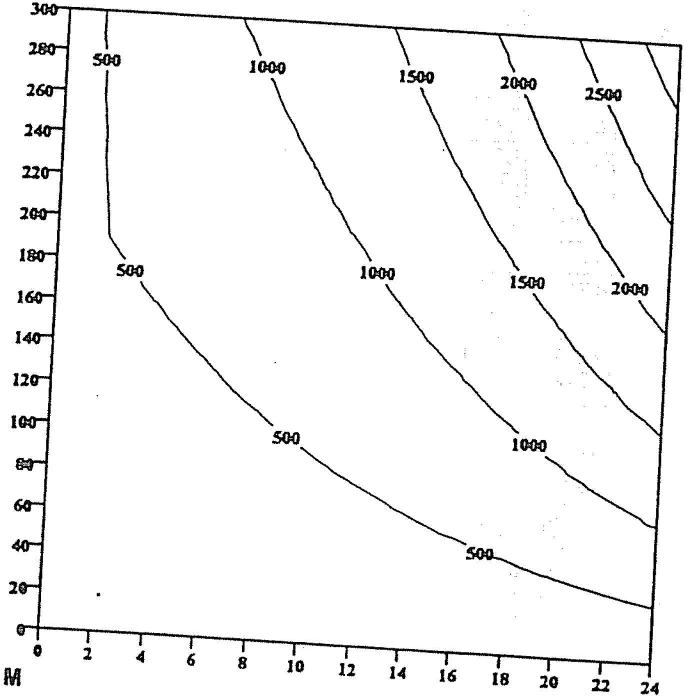
$Rstd(T,W) := ar \cdot W^{br} \cdot \exp(cr \cdot T)$

$M_{i,j} = Rstd\left(T_i, W_j\right)$

$$Lr_{\left(W_j\right)} := \left(\frac{W_j}{aLr}\right)^{\left(\frac{1}{bLr}\right)}$$

T_i	W_j	$Lr_{\left(W_j\right)}$	$Rstd\left(T_i, W_j\right)$
2	0	0	0
4	10	93	50
6	20	118	86
8	30	135	118
10	40	149	147
12	50	161	176
14	60	171	203
16	70	180	229
18	80	189	254
20	90	196	278
22	100	203	302
24	110	210	326
	120	216	349
	130	222	371
	140	228	394
	150	233	415
	160	238	437
	170	243	458
	180	248	479
	190	253	500
	200	257	520
	210	261	541
	220	265	561
	230	269	581
	240	273	600
	250	277	620
	260	281	639
	270	284	658
	280	288	677
	290	291	696
	300	295	715
			0
			57
			98
			135
			169

—This Rstd value of 50 is for T = 2 C and W = 10.0 g



The remaining elements of this array have been cut off.

Filename: RATE-T.MCD Version: August 10, 1995 Equations 5-13 and 6-5

The purpose of this worksheet is to evaluate side-by-side the temperature functions for maximum consumption (Cmax) and standard respiration (Rstd), denoted below as f1T and f2T, respectively. f1T is restricted to the interval [0,1]; f2T increases from 1.0 at T=0 C. The paramater values for f1T differ for BT and RT, where as the parameter values for f2T are the same for both species. Below I have used the RT parameter values for f1T.

$T := 0, 1 .. 25$

$T1 := 4.0 \qquad T2 := 15.0 \qquad T3 := 22.0 \qquad T4 := 24.0$

$T1K := 0.20 \qquad T2K := 0.70 \qquad T3K := 0.98 \qquad T4K := 0.20$

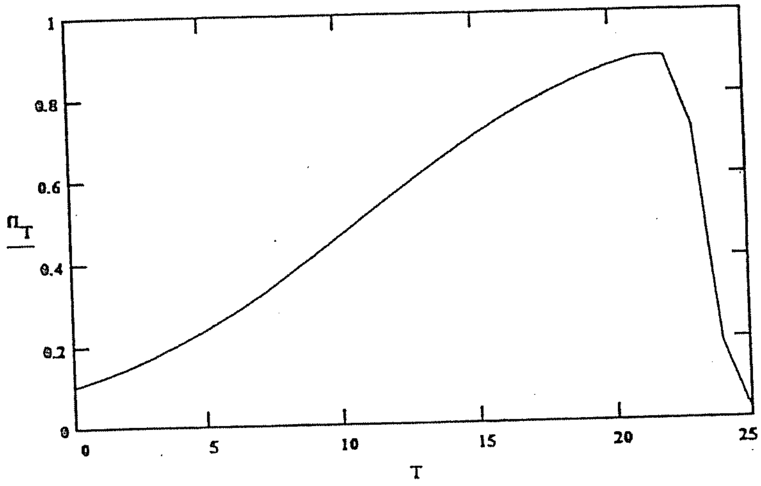
$$A_T := \frac{1.0}{T2 - T1} \cdot \ln\left[\frac{T2K \cdot (1.0 - T1K)}{T1K \cdot (1.0 - T2K)}\right] \qquad B_T := \frac{1.0}{T4 - T3} \cdot \ln\left[\frac{T3K \cdot (1.0 - T4K)}{T4K \cdot (1.0 - T3K)}\right]$$

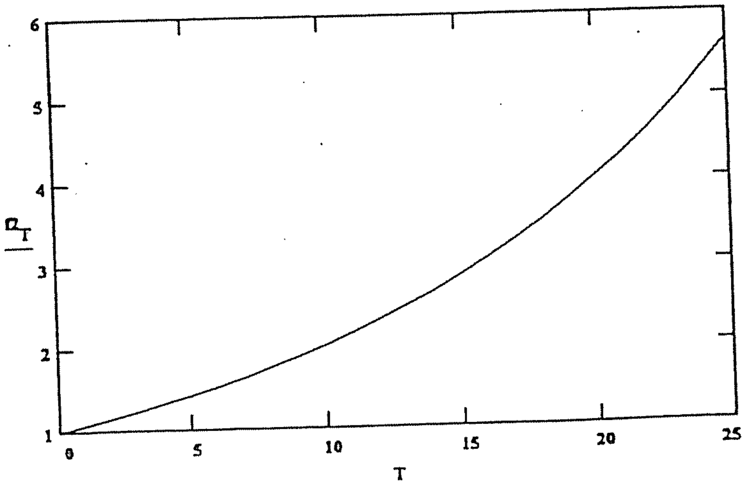
$$KA_T := \frac{T1K \cdot \exp\left[A_T \cdot (T - T1)\right]}{1.0 + T1K \cdot \left[\exp\left[A_T \cdot (T - T1)\right] - 1.0\right]} \quad KB_T := \frac{T4K \cdot \exp\left[B_T \cdot (T4 - T)\right]}{1.0 + T4K \cdot \left[\exp\left[B_T \cdot (T4 - T)\right] - 1.0\right]} \quad f1_T := KA_T \cdot KB_T$$

Now for the temperature function for standard respiration.

$cR := 0.0693 \qquad f2_T := \exp(cR \cdot T)$

T	$f1_T$	$f2_T$
0	0.1	1
1	0.12	1.072
2	0.143	1.149
3	0.169	1.231
4	0.2	1.319
5	0.234	1.414
6	0.273	1.516
7	0.315	1.624
8	0.36	1.741
9	0.408	1.866
10	0.458	2
11	0.509	2.143
12	0.559	2.297
13	0.609	2.462
14	0.656	2.638
15	0.7	2.828
16	0.741	3.031
17	0.778	3.248
18	0.811	3.481
19	0.84	3.731
20	0.866	3.999
21	0.886	4.286
22	0.888	4.593
23	0.717	4.923
24	0.187	5.276
25	0.017	5.655





Filename: Ract.MCD **Version: August 10, 1995** **Equation 6-5**

The purpose of this file is to compare the magnitude of the temperature factor and the velocity (or swimming-speed) factor for activity metabolism. The equation used by Stewart et al. (1983), Rand et al. (1993), and us is as follows: Ract = (a*W**b)*exp(c*T)*exp(d*V). W has units of grams wet body weight, T is in deg C, and V is in cm/s. Units of "a" are grams of O2 consumed per day; in our model the value of "a" = 0.0022 is converted to 7.13 calories consumed per day.

PUB	a	b	c	d
Stewart et al.	0.00463	0.705	0.059	0.0232
Rand et al.	0.00264	0.793	0.0682	0.0234
WVW et al.	0.0022	0.784	0.0693	0.0300

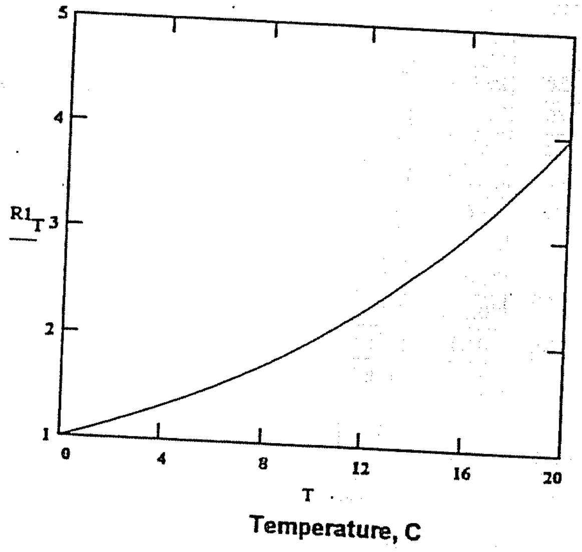
The Stewart et al. values are for lake trout in the Great Lakes; Rand et al. values are for steelhead in the Great Lakes; ours are for BT and RT in a small stream. Temperature range for Great Lakes that they considered was ca. 3-15 C; we need T up to ca. 22 C. Velocity range they considered was 10-60 cm/s or 0.6 to 3.0 body lengths per second. Note that 3.0 BL/s for a 20-cm (=200-mm) fish = 60 cm/s.

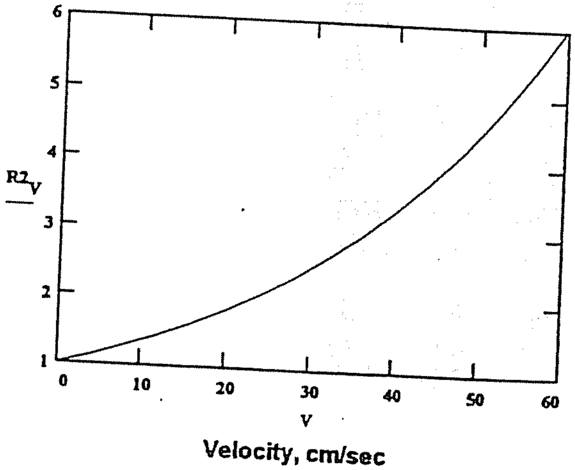
The brief analysis below is a comparison of the T factor and V factor using our parameter values. The take-home lesson is that these two factors are of approximately the same importance in terms of their influencing the value of activity respiration, Ract.

$c := 0.0693$ $d := 0.0300$ $T := 0, 1 .. 20$ $V := 0, 4 .. 60$

$R1_T := \exp(c \cdot T)$ $R2_V := \exp(d \cdot V)$

T	$R1_T$	V	$R2_V$
0	1	0	1
1	1.07	4	1.13
2	1.15	8	1.27
3	1.23	12	1.43
4	1.32	16	1.62
5	1.41	20	1.82
6	1.52	24	2.05
7	1.62	28	2.32
8	1.74	32	2.61
9	1.87	36	2.94
10	2	40	3.32
11	2.14	44	3.74
12	2.3	48	4.22
13	2.46	52	4.76
14	2.64	56	5.37
15	2.83	60	6.05
16	3.03		
17	3.25		
18	3.48		
19	3.73		
20	4		





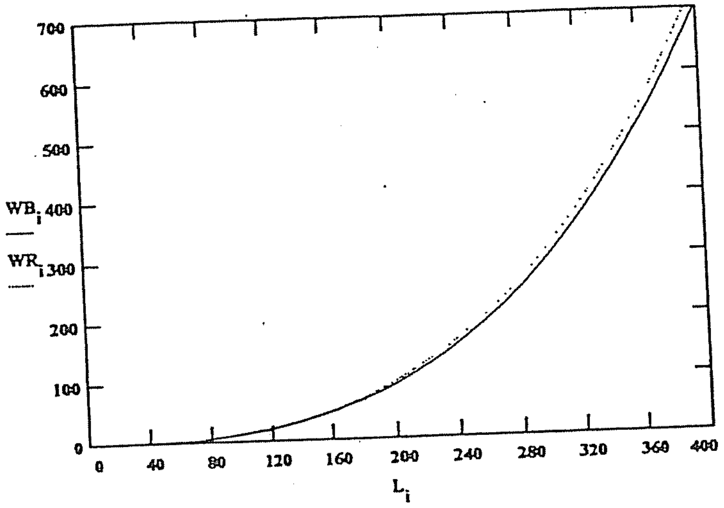
Filename: W-LREG.MCD   Version: August 10, 1995   Equation 6-6

The purpose of this worksheet is to illustrate the weight-length regression equations used in the trout model. The parameter values for these equations are based on W-L data from the Tule River for all ages, including Age 0. These values will be updated as necessary in light of the values in Studley et al. (1995, Appendix P; in press). W is wet weight of the trout in grams. L is fork length of the trout in mm. B denotes brown trout, and R denotes rainbow trout.. 40 $L_i := 10 \cdot i$

Brown Trout: $aB := 0.0000132$ $bB := 2.97$ $WB_i := aB \cdot (L_i)^{bB}$

Rainbow Trout: $aR := 0.0000147$ $bR := 2.96$ $WR_i := aR \cdot (L_i)^{bR}$

L_i	WB_i	WR_i
10	0	0
20	0.1	0.1
30	0.3	0.3
40	0.8	0.8
50	1.5	1.6
60	2.5	2.7
70	4	4.3
80	5.9	6.3
90	8.4	9
100	11.5	12.2
110	15.3	16.2
120	19.8	21
130	25.1	26.6
140	31.2	33.1
150	38.3	40.6
160	46.4	49.1
170	55.6	58.8
180	65.9	69.7
190	77.4	81.7
200	90.1	95.1
210	104.1	109.9
220	119.6	126.2
230	136.4	143.9
240	154.8	163.2
250	174.8	184.2
260	196.4	206.8
270	219.6	231.3
280	244.7	257.6
290	271.6	285.8
300	300.3	315.9
310	331.1	348.1
320	363.8	382.4
330	398.6	418.9
340	435.6	457.6
350	474.7	498.6
360	516.2	542
370	559.9	587.8
380	606.1	636
390	654.7	686.9
400	705.8	740.3



Filename: PMORTTRT.MCD Version: Nov 12, 1995 Equations 8-1, 8-2, & 8-3

The purpose of this file is to illustrate our function for daily probability of mortality (Pmort). We assume that risks of mortality can be divided into two categories, i.e., those that are present 24 hours a day every day (e.g., disease and parasites) and those that are present primarily when a fish is active (e.g., predation). We assume that all mortality risks are greater (1) for a small versus a large fish and (2) for a fish in poor versus good physiological condition. Finally, a fish dies when its physiological condition decreases to the minimum required for survival, Kmin.

In the equations below the variable Z is a daily instantaneous mortality rate, Z24 is the instantaneous mortality rate for those risks present 24 hours a day, and Zact is the instantaneous mortality rate for those risks present primarily when a fish is active.

The condition-dependent factor (FK) is defined as the ratio (K1 - Kmin)/(K - Kmin) has a value of 1.0 when K >= K1, the value for the index of condition above which we assume that risks of mortality are independent of physiological condition. This ratio becomes a large number as K decreases toward Kmin, in which case Pmort approaches 1.0, which satisfies the constraint that a fish dies when K = Kmin.

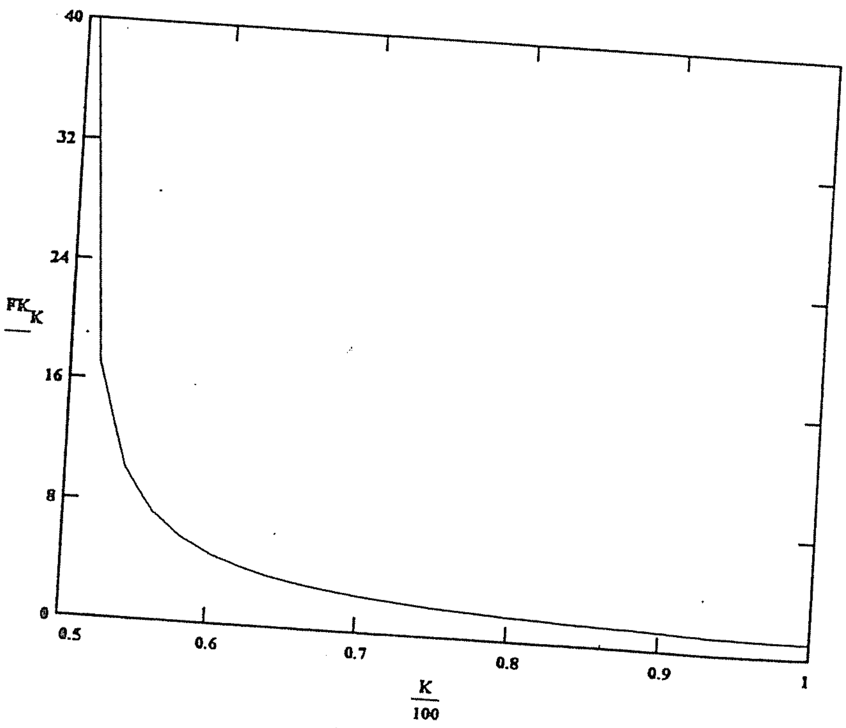
The length-dependent factor (FL) is a straight line with a negative slope to indicate that risks of mortality represented by both Z24 and Zact are assumed to decrease as length increases. The slope (aM) is that of a line connecting the two points having coordinates (L,FL) = (Lmin, 1.0) and (Lmax, FLmax). Thus, values for Z24, Zact, and FLmax are required to parameterize the function. The value for FLmax is between 0.0 and 1.0 and is interpreted as the relative decrease in risks of mortality for a large fish (Lmax) compared to a small fish (Lmin) for which FL has a value of 1.0. For a fish larger than Lmax, FL = FLmax.

The time-dependent variable D is the fraction of a day a fish is active.

First, we evaluate the condition-dependent factor (FK), then the length-dependent factor (FL), and finally the complete equation for the daily probability of mortality. Note: I am using Kmin = 49 here so that the function FK is defined at K = 50.

$\mathrm{Kmin} := 49 \quad \mathrm{Kmax} := 100 \quad K := 50, 52 .. 100 \quad FK_K := \dfrac{\mathrm{Kmax} - \mathrm{Kmin}}{K - \mathrm{Kmin}}$

$\frac{K}{100}$	FK_K
0.5	51
0.52	17
0.54	10.2
0.56	7.3
0.58	5.7
0.6	4.6
0.62	3.9
0.64	3.4
0.66	3
0.68	2.7
0.7	2.4
0.72	2.2
0.74	2
0.76	1.9
0.78	1.8
0.8	1.6
0.82	1.5
0.84	1.5
0.86	1.4
0.88	1.3
0.9	1.2
0.92	1.2
0.94	1.1
0.96	1.1
0.98	1
1	1



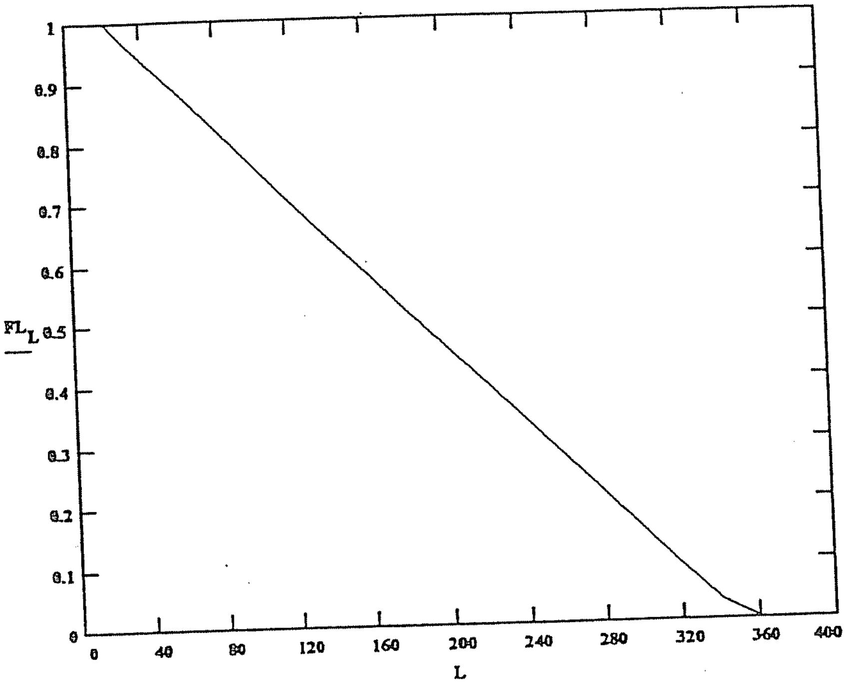
Page 2. Equations 8-1, 8-2, & 8-3, continued

Now for evaluation of the formulation for the length-dependent factor, FL.

$L := 20, 40 .. 400$ (mm FL) $Lmin := 20$ $Lmax := 350$ $FLmax := 0.001$

$$slope := \frac{FLmax - 1.0}{(Lmax - Lmin)} \qquad FL_L := if(L<Lmax, 1.0 + slope\cdot(L - 20), FLmax)$$

L	FL_L
20	1
40	0.94
60	0.88
80	0.82
100	0.76
120	0.7
140	0.64
160	0.58
180	0.52
200	0.46
220	0.39
240	0.33
260	0.27
280	0.21
300	0.15
320	0.09
340	0.03
360	0
380	0
400	0



Page 3. Equations 8-1, 8-2, & 8-3continued

In order to evaluate the complete function for the daily probability of mortality, Pmort, it is important to have a feel for the relation between values of annual probability of survival (PS), daily probability of mortality (Pmort=PM), and the daily instantaneous mortality rate (Z, units of 1/day). As shown below, values of PM and Z are very similar in the range of Z values we are using for Z24 and Zact.

$Z := 8, 9 .. 30 \quad Z1_Z := 0.0001 \cdot Z \quad PS_Z := \exp(-365 \cdot Z1_Z) \quad PM_Z := (1.0 - \exp(-Z1_Z))$

Z	$Z1_Z$	PS_Z	PM_Z
8	$8 \cdot 10^{-4}$	0.747	$7.997 \cdot 10^{-4}$
9	$9 \cdot 10^{-4}$	0.72	$8.996 \cdot 10^{-4}$
10	0.001	0.694	$9.995 \cdot 10^{-4}$
11	0.0011	0.669	0.001
12	0.0012	0.645	0.001
13	0.0013	0.622	0.001
14	0.0014	0.6	0.001
15	0.0015	0.578	0.001
16	0.0016	0.558	0.002
17	0.0017	0.538	0.002
18	0.0018	0.518	0.002
19	0.0019	0.5	0.002
20	0.002	0.482	0.002
21	0.0021	0.465	0.002
22	0.0022	0.448	0.002
23	0.0023	0.432	0.002
24	0.0024	0.416	0.002
25	0.0025	0.402	0.002
26	0.0026	0.387	0.003
27	0.0027	0.373	0.003
28	0.0028	0.36	0.003
29	0.0029	0.347	0.003
30	0.003	0.335	0.003

Page 4. Equations 8-1, 8-2, & 8-3 continued

OK. Now for the total function for Pmort.

Condition-dependent factor: $K := 50, 52 .. 100$ $Kmin := 49$ $Kmax := 100$ $FK_K := \frac{Kmax - Kmin}{K - Kmin}$

Length-dependent factor: $L := 20, 40 .. 400$ $FLmax := 0.001$ $Lmax := 350$ $Lmin := 20$ $slope := \frac{FLmax - 1.0}{(Lmax - Lmin)}$

$$FL_L := if(L<Lmax, 1.0 + slope \cdot (L - 20), FLmax)$$

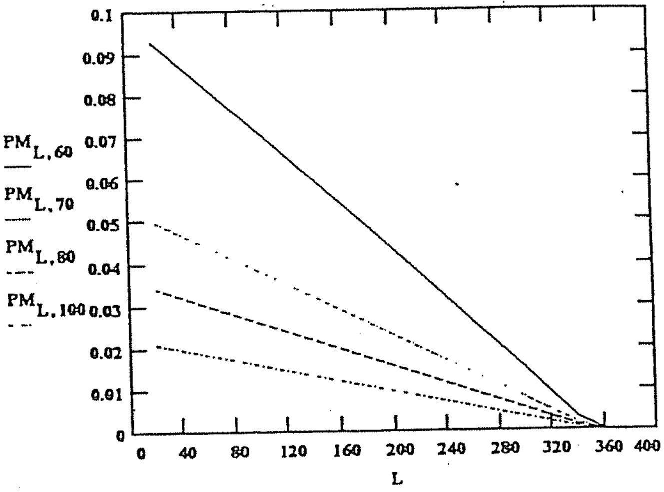
Sum of the two Z terms $Z24 := 0.001$ $Zact := 0.02$ $D := 1.0$ $Z := Z24 + D \cdot Zact$ $Z = 0.021$

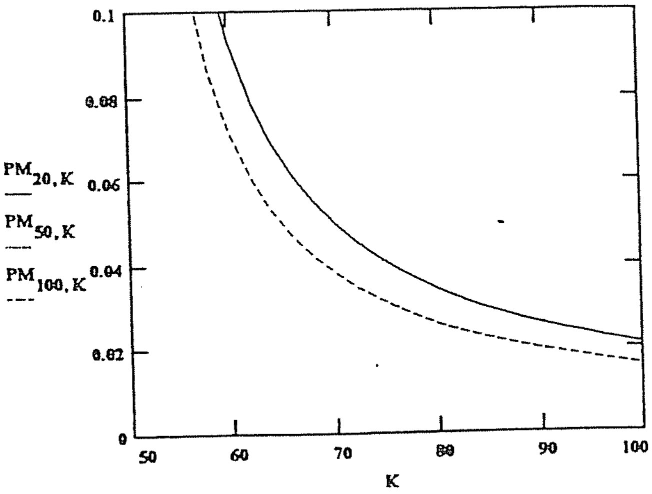
Complete equation: $PM_{L,K} := 1.0 - \exp\left(-FL_L \cdot FK_K \cdot Z\right)$

The two graphs below are slices through the response surface of PM as a fct of length of the trout and its condition factor. For example, in the top graph K is held constant at 60, 70, 80, or 100, and for each of these four K values the value of PM is calculated for lengths between 20 and 300 mm. Note that K values are on a percentage scale here, rather than 5 to).

K	FK_K
50	51
52	17
54	10.2
56	7.3
58	5.7
60	4.6
62	3.9
64	3.4
66	3
68	2.7
70	2.4
72	2.2
74	2
76	1.9
78	1.8
80	1.6
82	1.5
84	1.5
86	1.4
88	1.3
90	1.2
92	1.2
94	1.1
96	1.1
98	1
100	1

L	FL_L	$PM_{L,60}$	$PM_{L,100}$
20	1	0.093	0.021
40	0.94	0.087	0.02
60	0.88	0.082	0.018
80	0.82	0.077	0.017
100	0.76	0.071	0.016
120	0.7	0.066	0.015
140	0.64	0.06	0.013
160	0.58	0.055	0.012
180	0.52	0.049	0.011
200	0.46	0.043	0.01
220	0.39	0.038	0.008
240	0.33	0.032	0.007
260	0.27	0.026	0.006
280	0.21	0.021	0.004
300	0.15	0.015	0.003
320	0.09	0.009	0.002
340	0.03	0.003	$6.565 \cdot 10^{-4}$
360	0	$9.736 \cdot 10^{-5}$	$2.1 \cdot 10^{-5}$
380	0	$9.736 \cdot 10^{-5}$	$2.1 \cdot 10^{-5}$
400	0	$9.736 \cdot 10^{-5}$	$2.1 \cdot 10^{-5}$





Filename: FISHMORT.MCD Version: August 10, 1995 Equation 8-5

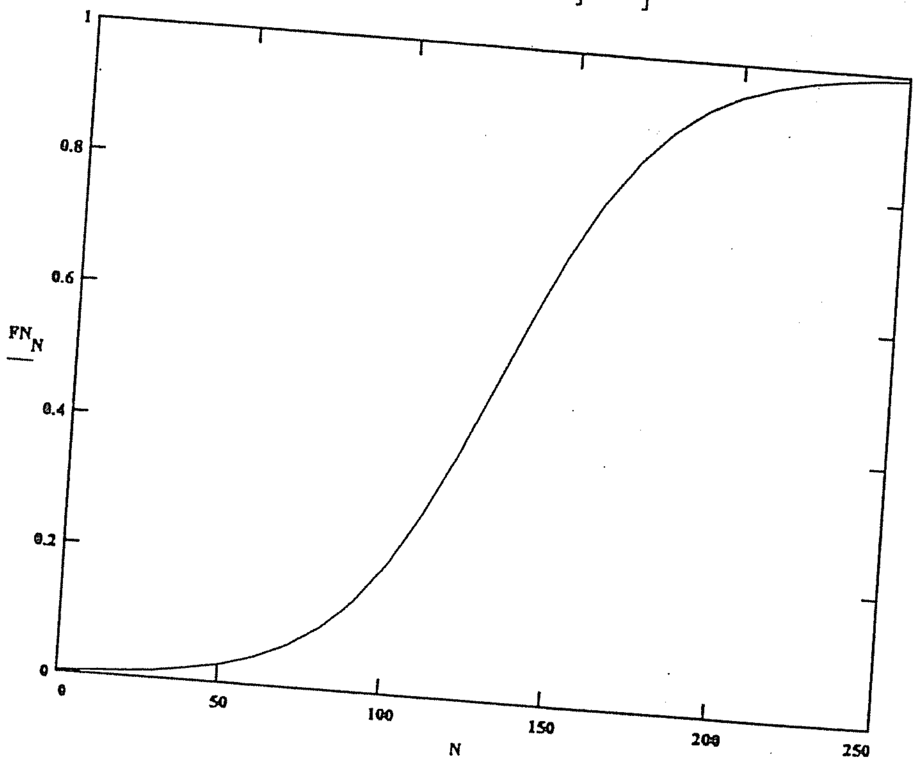
The history of stocking hatchery trout in the United States and other countries clearly indicates that fishing effort and mortality increase whenever and wherever stocking occurs (Moring 1993; Vincent 1987). Thus, we represent the density-dependent multiplier (FN) as a logistic function of the density of trout; this function approaches 0.0 at low values of N and 1.0 at high values of N. We require that this function pass through the two points (N1, FN1) and (N2, FN2). The coordinates for these two points are selected based on a combination of empirical data and expert judgement. Our values are (100 trout/100 m, 0.20) and (200 trout/100 m, 0.95). The 100 trout/100 m is based on the average density of Age 1 and older brown and rainbow trout in Segment 8 of the Tule River. The 200 trout/100 m is double this average density and allows for stocking of hatchery rainbow trout on a weekly basis. The Y-axis coordinates for these two densities (i.e., 0.20 and 0.95) are selected to ensure that the function for FN covers nearly all the range between 0.0 and 1.0.

$N := 0, 10 .. 250 \qquad N1 := 100 \qquad N2 := 200$

$FN1 := 0.20 \qquad FN2 := 0.95$

$$A_N := \frac{1.0}{N2 - N1} \cdot \ln\left[\frac{FN2 \cdot (1.0 - FN1)}{FN1 \cdot (1.0 - FN2)}\right] \qquad FN_N := \frac{FN1 \cdot \exp\left[A_N \cdot (N - N1)\right]}{1.0 + FN1 \cdot \left[\exp\left[A_N \cdot (N - N1)\right] - 1.0\right]}$$

N	FN_N
0	0.003
10	0.005
20	0.008
30	0.012
40	0.018
50	0.028
60	0.042
70	0.064
80	0.095
90	0.14
100	0.2
110	0.278
120	0.373
130	0.478
140	0.586
150	0.685
160	0.771
170	0.838
180	0.889
190	0.925
200	0.95
210	0.967
220	0.978
230	0.986
240	0.991
250	0.994



APPENDIX 5 INPUT DATA FILES

This appendix includes samples of the five input data files used by the trout model. These files are in addition to file INPUT.DAT in Appendix 1.

Table A5-1. Sample Input File with Daily Average Flow Data

Year	Day	Flow (cfs)
1984	275	2.2
1984	276	2.2
1984	277	2.2
1984	278	2.2
1984	279	2.2
1984	280	2.2
1984	281	2.0
1984	282	2.0
.	.	.
.	.	.
.	.	.
1993	242	14.0
1993	243	14.0
1993	244	14.0
1993	245	14.0
1993	246	13.0
1993	247	13.0
1993	248	13.0
1993	249	9.0
1993	250	1.9
1993	251	1.9
1993	252	1.8
1993	253	1.8
1993	254	1.8
1993	255	1.8
1993	256	1.4
1993	257	1.9
1993	258	2.1
1993	259	2.1
1993	260	2.1
1993	261	2.1
1993	262	2.1
1993	263	2.1
1993	264	2.1
1993	265	2.1
1993	266	2.1
1993	267	2.1
1993	268	2.0
1993	269	2.0
1993	270	2.0
1993	271	1.9
1993	272	1.9
1993	273	1.9

Table A5-2. Sample Input File with Average Daily Temperature Data.

Year	Day	Temperature (°C)
1986	1	4.0
1986	2	3.6
1986	3	3.7
1986	4	4.2
1986	5	5.1
1986	6	4.3
1986	7	4.2
1986	8	4.1
1986	9	4.3
1986	10	4.4
1986	11	4.3
1986	12	4.2
1986	13	4.8
1986	14	4.8
1986	15	4.3
1986	16	4.1
.	.	.
.	.	.
.	.	.
1993	328	5.2
1993	329	4.4
1993	330	4.4
1993	331	5.4
1993	332	6.4
1993	333	6.0
1993	334	5.4
1993	335	4.8
1993	336	5.1
1993	337	5.1
1993	338	5.0
1993	339	4.5
1993	340	4.4
1993	341	4.1
1993	342	4.3
1993	343	4.3
1993	344	4.8
1993	345	3.9
1993	346	2.5
1993	347	3.5
1993	348	2.9
1993	349	2.1
1993	350	2.2
1993	351	2.6
1993	352	2.7
1993	353	3.0

Table A5-3. Characteristics of the Initial Brown and Rainbow Trout Populations

Characteristics of the brown and rainbow trout populations based on the Summer and Fall electrofishing population surveys in Segment 8 of the North Fork Middle Fork Tule River, California, for the years 1987 through 1992 (Studley et al. 1995). The first line in each block indicates the year, number of brown trout (all ages combined) per 100 meters, number of rainbow trout (all ages combined) per 100 meters, and the season (i.e., summer or fall). The column headings are defined as follows:

density: number of trout per 100 meters of stream length.
total: density times 1,035 meters in Segment 8.
fractn: total for each age class divided by total for all ages combined.
lmode: average fork length (mm) of trout in each age class.

Columns 2-5 are for brown trout; columns 6-9 are for rainbow trout. For the simulations presented in this report, we used the Fall 1987 and Fall 1990 results to characterize the initial brown and rainbow trout populations in the model as of October 1.

Parameters in the INPUT.DAT file relating to initial populations are as follows:

ptrack	Proportion of the Age 0 brown and rainbow trout populations to follow in the simulation model as individuals. Value varies depending on the purpose of the simulation.
stdlen(i)	Used to calculate minimum and maximum of a symmetrical triangular distribution for the length of trout in each age class for brown trout and native rainbow trout. The triangular distribution is centered on lmode (see above). Value: 0.2 (BT); 0.2 (RT)
wtdev(i)	Standard error used to calculate initial weight (g wet wt) of each model trout based on its length (mm). Value: 0.043 (BT); 0.078 (RT).

```
1987         58     489     summer      estimated pop. fish/100m  tule  segment 8
     density  total   fractn    lmode        density  total    fractn    lmode
0+     40.5    419.    0.69      64.          378.0   3912.     0.77      42.
1+      2.0     21.    0.03     133.           97.5   1009.     0.20     112.
2+     11.0    114.    0.19     181.           12.5    129.     0.03     159.
3+      4.0     41.    0.07     224.            1.5     16.     0.00     251.
4+      1.0     10.    0.02     352.            0.0      0.     0.00       0.
5+      0.0      0.    0.00     453.            0.0      0.     0.00       0.

1987         46     248      fall       estimated pop. fish/100m  tule  segment 8
     density  total   fractn    lmode        density  total    fractn    lmode
0+     36.0    373.    0.78      95.          200.5   2075.     0.81      77.
1+      3.5     36.    0.08     162.           43.0    445.     0.17     123.
2+      5.5     57.    0.12     209.            3.5     36.     0.01     175.
3+      1.0     10.    0.02     250.            1.5     16.     0.01     233.
4+      0.0      0.    0.00     352.            0.0      0.     0.00       0.
5+      0.0      0.    0.00     453.            0.0      0.     0.00       0.

1988        153     652     summer      estimated pop. fish/100m  tule  segment 8
     density  total   fractn    lmode        density  total    fractn    lmode
0+    128.0   1325.    0.84      60.          553.0   5724.     0.85      37.
1+     16.5    171.    0.11     146.           92.5    957.     0.14     114.
2+      4.0     41.    0.03     201.            7.0     72.     0.01     162.
3+      4.5     47.    0.03     231.            0.0      0.     0.00     251.
4+      0.0      0.    0.00     338.            0.0      0.     0.00       0.
5+      0.0      0.    0.00     364.            0.0      0.     0.00       0.
```

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1988        114      253      fall      estimated pop.   fish/100m   tule   segment 8
     density    total    fractn    lmode      density    total    fractn    lmode
0+    100.0     1035.     0.87      93.        210.0     2174.     0.83      72.
1+      9.0       93.     0.08     161.         37.5      388.     0.15     126.
2+      4.0       41.     0.03     216.          5.5       57.     0.02     158.
3+      1.5       16.     0.01     242.          0.0        0.     0.00     251.
4+      0.0        0.     0.00     352.          0.0        0.     0.00       0.
5+      0.0        0.     0.00     452.          0.0        0.     0.00       0.
1989        165      558      summer    estimated pop.   fish/100m   tule   segment 8
     density    total    fractn    lmode      density    total    fractn    lmode
0+    114.5     1185.     0.69      60.        440.0     4554.     0.79      40.
1+     42.5      440.     0.26     144.        100.0     1035.     0.18     113.
2+      6.0       62.     0.04     193.         18.0      186.     0.03     151.
3+      2.5       26.     0.02     220.          0.0        0.     0.00     251.
4+      0.0        0.     0.00     352.          0.0        0.     0.00       0.
5+      0.0        0.     0.00     470.          0.0        0.     0.00       0.
1989        117      245      fall      estimated pop.   fish/100m   tule   segment 8
     density    total    fractn    lmode      density    total    fractn    lmode
0+     94.5      978.     0.81      92.        185.0     1915.     0.76      72.
1+     18.5      191.     0.16     159.         51.5      533.     0.21     119.
2+      1.5       16.     0.01     194.          8.0       83.     0.03     163.
3+      2.5       26.     0.02     234.          0.5        5.     0.00     211.
4+      0.0        0.     0.00     352.          0.0        0.     0.00       0.
5+      0.0        0.     0.00     470.          0.0        0.     0.00       0.
1990        204      324      summer    estimated pop.   fish/100m   tule   segment 8
     density    total    fractn    lmode      density    total    fractn    lmode
0+    143.5     1485.     0.70      55.        181.0     1873.     0.56      40.
1+     46.5      481.     0.23     142.        134.0     1387.     0.41     108.
2+     13.5      140.     0.07     205.          9.5       98.     0.03     156.
3+      1.0       10.     0.00     231.          0.0        0.     0.00     251.
4+      0.0        0.     0.00     352.          0.0        0.     0.00       0.
5+      0.0        0.     0.00     500.          0.0        0.     0.00       0.
1990        138      181      fall      estimated pop.   fish/100m   tule   segment 8
     density    total    fractn    lmode      density    total    fractn    lmode
0+     96.5      999.     0.70      92.         97.5     1009.     0.54      75.
1+     28.5      295.     0.21     155.         80.5      833.     0.44     120.
2+     11.0      114.     0.08     190.          3.0       31.     0.02     177.
3+      2.0       21.     0.01     244.          0.0        0.     0.00     251.
4+      0.0        0.     0.00     352.          0.0        0.     0.00       0.
5+      0.0        0.     0.00     400.          0.0        0.     0.00       0.
1991         78      148      summer    estimated pop.   fish/100m   tule   segment 8
     density    total    fractn    lmode      density    total    fractn    lmode
0+      9.5       98.     0.12      47.         96.0      994.     0.65      34.
1+     51.0      528.     0.65     127.         45.5      471.     0.31     117.
2+     15.5      160.     0.20     184.          6.5       67.     0.04     159.
3+      2.5       26.     0.03     238.          0.0        0.     0.00     251.
4+      0.0        0.     0.00     352.          0.0        0.     0.00       0.
5+      0.0        0.     0.00     400.          0.0        0.     0.00       0.
1991         43       93      fall      estimated pop.   fish/100m   tule   segment 8
     density    total    fractn    lmode      density    total    fractn    lmode
0+      8.0       83.     0.18      84.         56.5      585.     0.61      72.
1+     20.5      212.     0.47     141.         32.5      336.     0.35     122.
2+      8.5       88.     0.20     178.          4.0       41.     0.04     166.
3+      6.5       67.     0.15     207.          0.0        0.     0.00     251.
4+      0.0        0.     0.00     248.          0.0        0.     0.00       0.
5+      0.0        0.     0.00     401.          0.0        0.     0.00       0.
```

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1992        263     316     summer     estimated pop.  fish/100m  tule segment 8
      density    total    fractn    lmode        density   total     fractn    lmode
0+     242.5     2510.     0.92      63.          258.0    2670.      0.82      44.
1+       4.5       47.     0.02     139.           50.5     523.      0.16     124.
2+      13.0      135.     0.05     192.            7.5      78.      0.02     160.
3+       3.5       36.     0.01     237.            0.5       5.      0.00     200.
4+       0.0        0.     0.00     352.            0.0       0.      0.00       0.
5+       0.0        0.     0.00     420.            0.0       0.      0.00       0.

1992        185     151      fall      estimated pop.  fish/100m  tule segment 8
      density    total    fractn    lmode        density   total     fractn    lmode
0+     173.0     1791.     0.93      88.          118.5    1226.      0.78      73.
1+       2.5       26.     0.01     157.           28.5     295.      0.19     128.
2+       6.0       62.     0.03     200.            4.0      41.      0.03     163.
3+       4.0       41.     0.02     230.            0.0       0.      0.00     200.
4+       0.0        0.     0.00     352.            0.0       0.      0.00       0.
5+       0.0        0.     0.00     520.            0.0       0.      0.00       0.
```

Table A5-4. Sample Input File with Habitat Mapping Data for Segment 8 of the North Middle Fork Tule River, California

The column headings are defined as follows:

id	Identification number of the habitat unit used by PG&E
stn	Location of the upstream boundary of the habitat unit along a distance scale that starts upstream of Segment 8
len	Length (m) of the habitat unit at base flow
pg&3 type	Habitat type as classified by pg&e; brs = bedrock chute, cas = cascade, hgr = high gradient, pool = pool, pw = pocketwater, rif = riffle, run = run
width	Average width (m) of the habitat unit at base flow.
ornl type	Habitat type as classified by ornl; cas = cascade, pool = pool, pw = pocketwater, rif = riffle, run = run
notes codes	Not used
donor transect	Numbers 1,..., 10 indicate which of the ten PHABSIM transects were used to characterize habitat units not having a PHABSIM transect. Cascade habitat units are not assigned a transect.
depth	Average depth (cm) of the habitat unit at base flow
spawn hab	Percentage of the habitat unit with substrate suitable for spawning
bld cov	Percentage of the habitat unit with boulder cover
tot cov	Percentage of the habitat unit with cover of any type

	id	stn (m)	len (m)	pg&e type	width (m)	ornl type	notes codes	donor transect		depth (cm)	spawn hab	bld cov	tot cov
1	146	1789.2	22	pw	3.0	pw		t	9	15	1	12	17
2		1790.4	1	cas	1.2	cas	1	x		0	0	0	0
3		1795.9	5	pool	2.7	pool	3	t	7	30	1	12	14
4		1798.6	3	cas	4.3	cas	0	x		0	0	0	0
5	150	1805.6	7	pw	2.1	pw	10	t	8	25	1	10	14
6		1807.5	2	cas	1.2	cas	2	x		0	0	0	0
7		1809.3	2	pool	7.3	pool	3	t	2	46	3	1	16
8	153	1814.8	7	brs	0.9	cas	2	x		0	0	0	0
9	155	1830.6	14	pool	6.1	pool	3	t	4	30	3	12	17
10		1832.2	5	cas	0.0	cas	2	x		0	0	0	0
11		1854.1	19	pool	7.6	pool	3	t	1	61	7	5	14
12	158a	1854.7	1	x	5.0	cas	1	x		0	0	0	0
13		1866.9	12	pw	3.0	pw	3	t	8	25	0	7	14
14	160	1868.4	2	cas	0.0	cas	2	x		0	0	0	0
15		1878.2	10	pw	3.0	pool	3	t	7	23	0	10	13
16		1886.1	8	cas	0.0	cas	2	x		0	0	0	0
17		1904.1	18	pool	5.5	pool	7	t	6	46	5	12	24
18		1910.8	7	run	2.4	pw	3	t	7	25	1	10	11
19	165	1926.3	16	pw	9.1	pw	9	t	8	30	1	10	15
20		1928.8	2	cas	1.8	cas	1	x		0	0	0	0
21		1934.0	5	pw	2.7	pw	7	t	8	25	2	10	11
22		1936.7	3	rif	1.8	rif		t	3	15	0	5	6
23		1942.2	5	run	3.0	rif	3	t	3	23	1	5	7
24	170	1946.5	4	pw	3.7	pw	9	t	8	20	0	5	5
25		1951.9	5	cas	5.5	cas	2	x		0	0	0	0
26		1954.7	3	pw	2.7	pool	3	t	7	30	0	40	42
27		1960.8	6	brs	0.8	run	3	x		61	0	0	0
28		1980.9	20	pool	7.9	pool		t	2	46	2	12	17
29	175	1989.7	9	rif	3.7	rif		t	10	10	1	2	3
30		1998.9	9	pool	4.3	pool		t	4	20	1	6	7
31		2004.1	5	brs	1.8	cas	1	x		0	0	0	0
32		2011.4	7	pw	3.0	pw		t	9	15	3	10	12
33		2015.0	4	rif	6.1	rif		t	3	10	1	2	4
34	180	2020.8	6	pool	3.4	pool		t	6	41	1	15	16
35		2026.6	6	pw	3.0	pw		t	8	28	0	12	13

36		2035.8	9	pw	7.6	pw		t	9	18	1	10	13
37		2037.0	1	cas	4.3	cas	0	x		0	0	0	0
38		2043.4	6	pw	3.7	pw		t	8	30	1	7	9
39	185	2045.2	2	brs	0.9	cas	0	x		0	0	0	0
40	186a	2048.3	3	x	2.4	run		t	7	30	2	2	5
41	187a	2053.1	5	x	2.4	pool		t	7	30	2	2	5
42		2056.2	3	rif	1.8	rif		t	3	15	0	2	3
43		2059.2	3	run	1.8	rif		t	3	20	0	2	3
44		2060.1	1	rif	1.5	rif		t	5	10	0	1	2
45	190	2077.5	17	pw	3.7	pw		t	9	15	3	12	15
46		2081.8	4	cas	7.3	cas	2	x		0	0	0	0
47		2088.5	7	pw	3.0	pool		t	7	46	1	10	11
48		2101.0	12	pool	5.5	pool	4	t	1	56	2	5	11
49		2106.8	6	cas	6.1	cas	2	x		0	0	0	0
50	195	2112.0	6	pw	3.7	pw	7	t	8	28	0	5	7
51		2123.2	8	pool	4.6	pool		t	4	30	1	7	14
52		2125.4	2	cas	0.3	cas	2	x		0	0	0	0
53		2135.4	10	pw	5.5	pw	11	t	8	30	1	8	10
54	200	2145.5	10	rif	3.7	rif	11	t	5	15	1	5	8
55		2157.4	12	pw	3.7	pw	10	t	8	30	4	5	8
56		2166.8	9	pool	5.5	pool	11	t	6	46	4	7	8
57		2175.4	9	pw	5.5	pw		t	8	23	1	10	12
58		2183.0	8	run	2.4	rif		t	3	25	0	5	6
59	205	2188.2	5	pool	3.7	pool		t	4	15	3	4	4
60		2191.8	4	rif	2.4	rif		t	10	10	1	4	6
61		2196.7	5	pool	3.7	pool		t	4	30	1	3	5
62		2212.5	16	rif	3.7	rif		t	5	10	2	5	8
63		2218.6	6	pool	4.3	pool		t	4	25	1	7	10
64	210	2228.7	10	pw	5.5	pw		t	9	18	2	10	12
65		2241.2	12	rif	5.5	rif		t	3	13	2	5	7
66		2257.7	16	rif	6.1	rif		t	3	18	0	0	0
67		2263.7	6	cas	0.9	cas	2	x		0	0	0	0
68		2279.0	15	pool	5.3	pool		t	2	51	2	30	35
69	215	2297.3	18	rif	2.7	rif	6	t	3	15	0	7	12
70		2307.9	11	pool	5.5	pool	3	t	1	46	1	8	12
71		2311.3	3	rif	2.4	rif		t	10	15	0	0	0
72	217a	2312.3	1	x	1.0	cas	1	x		0	0	3	4
73		2324.7	12	pool	5.5	pool	7	t	6	38	2	5	8
74		2327.8	3	rif	3.7	rif		t	5	8	0	5	6
75	220	2334.8	7	pool	5.5	pool	7	t	7	28	0	5	9
76		2349.7	15	pw	1.8	pw	9	t	9	23	1	7	10
77		2353.1	3	run	3.0	pw		t	9	18	0	6	6
78		2357.9	5	pool	3.0	pool	10	t	7	30	2	4	4
79		2364.3	6	rif	2.4	rif	8	t	10	13	1	5	6
80	225	2371.0	7	pool	3.7	pool	7	t	4	30	3	5	5
81		2371.6	1	cas	5.5	cas	1	x		0	0	0	0
82		2385.1	13	pw	5.5	pw	9	t	8	23	5	7	37
83		2392.1	7	cas	5.5	cas	2	x		0	0	0	0
84		2420.7	29	pw	1.8	pw	8	t	8	25	7	10	23
85	230	2434.1	15	pool	5.5	pool	3	t	6	36	6	10	12
86	231a	2437.2	10	x	5.5	cas	2	x		0	0	0	0
87		2440.5	5	rif	5.5	rif		t	3	15	0	10	11
88		2453.3	13	pool	5.5	pool	7	t	4	30	6	8	9
89		2455.5	2	cas	1.8	cas	1	x		0	0	0	0
90		2458.8	3	pool	2.4	pool	4	t	7	46	1	3	7
91	235	2460.3	2	cas	0.9	cas	2	x		0	0	0	0
92		2462.2	2	pool	5.5	pool		t	6	36	2	7	11
93		2463.4	1	rif	3.0	rif		t	5	5	4	0	0
94		2468.3	5	pool	4.3	pool		t	4	30	2	5	7
95		2472.8	5	rif	1.8	rif		t	10	20	0	3	4
96	240	2477.7	5	cas	3.7	cas	2	x		0	0	0	0
97		2490.8	13	pool	6.7	pool	4	t	1	61	4	12	15
98		2500.0	9	hgr	3.7	cas	2	x		0	0	4	5
99		2508.5	9	pool	5.5	pool	10	t	6	30	0	7	8
100		2516.7	8	rif	3.7	rif		t	3	18	1	4	5
101	245	2524.4	8	pw	2.4	pw	10	t	9	18	4	5	7
102		2526.2	2	hgr	3.7	cas	1	x		0	0	3	4
103		2564.0	38	pool	4.6	pool	7	t	6	46	8	15	17
104		2566.1	2	cas	3.4	cas	0	x		0	0	0	0
105	250	2570.7	5	pool	9.8	pool	7	t	2	46	3	25	30
106		2571.6	1	cas	4.3	cas	1	x		0	0	0	0
107		2580.1	9	pool	5.5	pool	4	t	6	36	1	5	6
108		2584.4	4	pw	4.3	pw		t	8	23	0	60	61

109		2589.3	5	cas	5.5	cas	2	x		0	0	0	0
110	255	2600.6	11	pool	5.5	pool		t	6	46	1	12	14
111		2620.4	20	cas	1.8	cas	2	x		0	0	0	0
112		2633.5	13	pw	4.9	pw	4	t	8	30	1	10	10
113		2636.5	3	cas	3.0	cas	1	x		0	0	0	0
114		2648.4	12	pool	4.6	pool		t	4	30	2	10	12
115	260	2652.4	4	cas	3.7	cas	2	x		0	0	0	0
116		2660.0	8	pool	7.3	pool		t	1	69	0	12	14
117		2661.5	2	cas	7.3	cas	1	x		0	0	0	0
118		2664.3	3	pool	6.1	pool		t	2	46	0	5	7
119		2670.4	6	pw	4.3	pw		t	8	30	0	7	7
120	265	2677.1	7	pool	3.7	pool	8	t	6	46	1	4	7
121		2683.2	6	hgr	2.4	cas	0	x		0	0	0	0
122		2713.0	30	pw	2.7	pw		t	8	23	1	7	10
123		2714.5	2	cas	3.7	cas	2	x		0	0	0	0
124		2728.0	13	pool	4.6	pool	11	t	6	46	1	7	11
125	270	2736.5	9	pw	3.7	pw	11	t	9	18	1	10	12
126		2753.6	17	cas	7.3	cas	0	x		0	0	0	0
127		2758.7	5	run	4.0	rif		t	3	15	1	2	8
128		2763.9	5	brs	1.8	cas	2	x		0	0	0	0
129		2767.9	4	pool	5.5	pool		t	6	46	3	5	12
130	274a	2768.8	1	x	0.0	cas	1	x		0	0	0	0
131	275	2792.9	24	pool	18.3	pool		t	1	91	7	7	23

Table A5-5. Sample Input File with PHABSIM Output Hydraulic Parameters. This input file is created by the user automatically as output from the standard PHABSIM software.

```
1.00  0.35234E+00  0.42852E+00
 1.00   1      0.0  0     47.60
 1.00   2      1.4  0     47.80
 1.00   3      1.6  0     47.50
 1.00   4      3.0  0     46.30
 1.00   5      4.0  0     46.30
 1.00   6      5.0  0     46.30
 1.00   7      6.0  0     46.30
 1.00   8      7.1  0     46.10
 1.00   9      8.0  1     46.10
 1.00  10      8.5  0     49.10
 1.00  11     15.0  0     49.10
 1.00  12     16.0  1     44.50
 1.00  13     17.0  2     44.30
 1.00  14     18.0  2     44.30
 1.00  15     19.0  2     44.20
 1.00  16     20.0  2     44.30
 1.00  17     21.0  2     43.90
 1.00  18     22.0  2     44.00
 1.00  19     23.0  2     44.00
 1.00  20     24.0  2     44.30
 1.00  21     25.0  2     46.00
 1.00  22     27.9  0     46.90
 1.00  23     29.0  0     46.50
 1.00  24     29.5  1     45.30
 1.00  25     31.0  1     45.30
 1.00  26     32.5  0     47.00
 1.00  27     32.7  0     47.50
 1.00  28     34.6  0     48.00
 1.00  29     36.3  0     48.20
2.00  0.31146E+00  0.57478E+00
 2.00   1      0.0  0     47.50
 2.00   2      4.0  0     47.40
 2.00   3      4.2  0     46.70
 2.00   4      6.5  0     46.20
 2.00   5      7.1  0     47.20
 2.00   6      9.0  0     47.20
 2.00   7     10.8  0     47.20
 2.00   8     11.6  2     46.10
 2.00   9     11.8  0     44.70
 2.00  10     13.0  1     44.50
 2.00  11     14.0  1     44.50
 2.00  12     15.0  0     44.50
 2.00  13     16.0  0     44.50
 2.00  14     17.0  1     44.50
 2.00  15     18.5  0     44.40
 2.00  16     19.0  0     44.40
 2.00  17     20.5  2     44.10
 2.00  18     21.0  2     44.00
 2.00  19     21.5  1     44.20
 2.00  20     22.0  2     44.20
 2.00  21     22.5  2     44.50
 2.00  22     23.0  2     44.70
 2.00  23     23.5  2     44.80
 2.00  24     24.0  2     44.80
 2.00  25     24.5  2     44.20
 2.00  26     25.0  2     44.00
 2.00  27     25.5  1     43.90
 2.00  28     26.0  1     43.80
 2.00  29     27.0  1     44.10
 2.00  30     28.0  0     45.10
 2.00  31     29.0  0     45.70
 2.00  32     30.0  0     45.90
 2.00  33     30.5  1     46.30
 2.00  34     31.1  0     47.10
 2.00  35     32.5  0     46.80
 2.00  36     32.7  0     47.60
 2.00  37     35.3  0     47.90
```

```
                                                         1.36
45.50   0.0025   29 2          8.75       0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 2.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 2.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 2.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 2.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 2.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.00000E+00   0.71925E+00
 8.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.30128E+00   0.00000E+00
 1.00   0.00000E+00   0.00000E+00   0.31981E+00   0.11146E+01
 4.00   0.66685E-01   0.87176E+00   0.31981E+00   0.11146E+01
 8.00   0.66685E-01   0.87176E+00   0.32922E+00   0.11549E+01
 4.00   0.66685E-01   0.87176E+00   0.31981E+00   0.11146E+01
 5.00   0.66685E-01   0.87176E+00   0.35668E+00   0.12717E+01
 7.00   0.66685E-01   0.87176E+00   0.46353E+00   0.12334E+01
 7.00   0.72535E-01   0.69085E+00   0.34765E+00   0.12334E+01
 7.00   0.66685E-01   0.87176E+00   0.42642E+00   0.11146E+01
 8.00   0.72535E-01   0.69085E+00   0.16670E+00   0.19117E+00
 8.00   0.72535E-01   0.69085E+00   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.00000E+00   0.65797E+01
 5.00   0.00000E+00   0.00000E+00   0.00000E+00   0.65797E+01
 7.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 7.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 6.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00
                                                         1.36
45.50   0.0025   39 2          8.75       0.00000E+00   0.00000E+00
 7.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.43748E+01   0.71925E+00
 8.00   0.10000E-01  -0.36970E-06   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.00000E+00   0.10319E+01
 2.00   0.00000E+00   0.00000E+00   0.00000E+00   0.51593E+00
 2.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 2.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 2.00   0.00000E+00   0.00000E+00   0.60256E+01   0.00000E+00
 2.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 2.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 2.00   0.00000E+00   0.00000E+00   0.54159E+00   0.11944E+01
 4.00   0.64814E-01   0.77286E+00   0.69529E+00   0.12334E+01
 4.00   0.72034E-01   0.58464E+00   0.17376E+00   0.00000E+00
 5.00   0.00000E+00   0.00000E+00   0.15493E+00   0.11549E+01
 5.00   0.36320E-01   0.18051E+01   0.40076E+00   0.10319E+01
 7.00   0.59456E-01   0.92664E+00   0.16039E+00   0.94562E+00
 7.00   0.39815E-01   0.16413E+01   0.14425E+00   0.90101E+00
 7.00   0.38536E-01   0.16995E+01   0.16645E+00   0.45050E+00
 7.00   0.11449E+00   0.99415E+00   0.43896E+00   0.11549E+01
 6.00   0.59456E-01   0.92664E+00   0.46353E+00   0.12334E+01
 5.00   0.59456E-01   0.92664E+00   0.00000E+00   0.12717E+01
 5.00   0.00000E+00   0.00000E+00   0.00000E+00   0.13094E+01
 4.00   0.00000E+00   0.00000E+00   0.00000E+00   0.11944E+02
 8.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.29429E+01   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00   0.00000E+00   0.00000E+00
 8.00   0.00000E+00   0.00000E+00
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APPENDIX 6 WORKSHOP PARTICIPANTS

This appendix lists the names and affiliations of individuals participating in the Workshop for the EPRI CompMech Trout Project, which was held in Sacramento, California, on December 5-7, 1994. The primary purpose of this workshop was to review the trout model.

Mike Aceituno, U. S. Fish & Wildlife Service, Sacramento, CA
Jean Baldrige, Trihey & Associates, Concord, CA
Jim Canaday, California State Water Resources Control Board, Sacramento, CA
Joe Cech, University of California-Davis, Davis, CA
Ed Cheslak, EA Engineering, Science, and Technology, Inc., Lafayette, CA
Mark Clark, University of Tennessee, Knoxville, TN
John Crandall, Occidental College, Los Angeles, CA
David Drake, California Department of Fish and Game, Garden Valley, CA
Tim Essington, University of Minnesota, St. Paul, MN
Gene Geary, Pacific Gas & Electric Co., San Ramon, CA
Tamara Grand, Simon Fraser University, Burnaby, British Columbia
Mike Henry, Federal Energy Regulatory Commission, Portland, OR
Steve Herrara, California State Water Resources Control Board, Sacramento, CA
Jennifer Hill, Federal Energy Regulatory Commission, Washington, DC
Karen Hockett, Virginia Polytechnic Institute and State University, Blacksburg, VA
Dave Hoopaugh, California Department of Fish and Game, Redding, CA
Henriette Jager, Oak Ridge National Laboratory, Oak Ridge, TN
Ralph Larson, San Francisco State University, San Francisco, CA
Peter Lickwar, U. S. Fish & Wildlife Service, Sacramento, CA
Donna Lindquist, Pacific Gas & Electric Co., San Ramon, CA
Brian Locke, University of Guelph, Guelph, Ontario
Dave Longanecker, Pacific Gas & Electric Co., San Ramon, CA
Dean Marston, California Department of Fish and Game, Fresno, CA
Kathleen Matthews, U. S. Forest Service, Albany, CA
Jack Mattice, Electric Power Research Institute, Palo Alto, CA
Dave McIntosh, Electric Power Research Institute, Palo Alto, CA
Tom McKenzie, California State Water Resources Control Board, Sacramento, CA
Dale Mitchell, California Department of Fish and Game, Fresno, CA
Sue Markie, California Department of Fish and Game, Rancho Cordova, CA
Peter Moyle, University of California-Davis, Davis, CA
Chris Myrick, University of California-Davis, Davis, CA
Jennifer Nielsen, Stanford University, Monterey, CA
David Noakes, University of Guelph, Guelph, Ontario
Bob Otto, R. G. Otto & Associates, Cambridge, MD
John Palmer, Southern California Edison, Rosemead, CA
Jim Petersen, National Biological Service, Cook, WA
Kathy Petersen, Pacific Gas & Electric Co., San Francisco, CA
Geoff Rabone, Southern California Edison, Rosemead, CA
Steve Railsback, Lang, Railsback & Associates, Arcata, CA

Gary Smith, California Department of Fish and Game, Sacramento, CA
Bill Snider, California Department of Fish and Game, Sacramento, CA
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Rob Titus, California Department of Fish and Game, Sacramento, CA
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Sam Williamson, National Biological Service, Ft. Collins, CO
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Ellen Yeoman, Pacific Gas & Electric Co., San Ramon, CA

ABOUT EPRI

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