Individual-based model of sympatric populations of brown and rainbow trout for instream flow assessment: model description and calibration

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Abstract

This paper describes an individual-based model of sympatric populations of brown and rainbow trout in a stream habitat. The model provides a tool for projecting flow and temperature effects on trout populations by linking the hydraulic component of the instream flow incremental methodology/physical habitat simulation system (IFIM/PHABSIM) to an individual-based population model. PHABSIM simulates the spatial distribution of depth and velocity at different flows, and indirectly, the availability of spawning habitat, cover and feeding station. The individual-based model simulates reproduction, growth and mortality of individual trout as a function of flow and temperature. Population dynamics arise from the survival and reproduction of individual trout. The spatially explicit nature of the model permits evaluation of behavioral responses used by fish to changes in physical habitat. The model has been calibrated to a stream segment in the North Fork Middle Fork Tule River, California. Selected parameters were adjusted to calibrate the model for length and abundance (including production of a new year class) at the end of 1-year simulations for each of 9 years. Predicted and observed lengths were in good agreement, although neither varied appreciably among years. Predicted and observed abundances were not in as good agreement, and differed considerably for some years. These differences reflect a combination of uncertainties in the field data and uncertainties in the model structure and parameter values. Fifty-year simulations indicated that model projections of length and abundance were stationary, although abundance values fluctuated considerably. Seven advantages for using simulation models of this type are emphasized. How to most effectively interpret results from such simulation models as part of instream flow environmental assessments remains a challenge. Variability and uncertainty in both field data and replicate model simulations are realities that have implications for scientists, resource managers, and regulators in

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projecting growth and abundance responses of fish populations to alternative flow or temperature regimes. © 1998 Elsevier Science B.V. All rights reserved.

1. Introduction

Trout and water diversions are the focus of numerous environmental assessments, monitoring studies, mitigation measures and regulatory decisions. Trout are common inhabitants of cold-water mountain streams and rivers, and they are highly valued by anglers. Many trout streams are also sites for water projects, which can alter the volume, timing and temperature of stream flows. Flow releases need to be managed in consideration of both the viability of the trout population and the economic benefits of water projects.

Changes in stream flow and temperature can affect trout in many ways, few of which are considered by the models typically used to support management decisions. A variety of models have been developed to provide a scientifically sound and objective decision framework for minimum instream flows, stream temperatures, trout habitat, trout populations and other biotic components of stream ecosystems (Stalnaker, 1993). The most widely used instream flow decision model (the physical habitat simulation system, PHABSIM) simulates how the area of 'usable' habitat varies with flow (Bovee, 1982; Milhous et al., 1989; Stalnaker, 1993). No explicit links between this habitat index and trout populations are made. The effects of alternative temperature regimes are typically assessed only by estimating how often a thermal criterion (e.g. 20°) is exceeded. Neither of these methods considers the potentially complex interactions between trout species and how these interactions may change with flow or temperature. Temperature assessment methods are also limited by considering the effects of high-temperature events only, whereas PHABSIM is applied only to habitat indices at 'average' or low flows without considering the potential population-limiting effects of extremely high flows.

The purpose of the model described in this paper is to allow population-level assessment of the effects of stream flow and temperature regimes on two sympatric trout species, considering biological interactions as well as habitat limitations. The model is intended for comparing the effects of alternative instream flow release schedules by water projects. The model can also be used to evaluate the complex effects of environmental changes such as climate warming (Jager et al., 1997b) and can provide a comprehensive framework for field studies of trout populations, including adaptive management of water projects (Van Winkle et al., 1997a).

Our modeling approach was guided by the questions commonly asked in assessing the effects of instream flows on fish populations and our knowledge concerning stream hydraulics and trout physiology, behavior and ecology. The model illustrates an application of the individual-based approach to population modeling (DeAngelis and Gross, 1992; Van Winkle et al., 1993; Jager et al., 1997a). We chose this approach because it is a relatively direct way to simulate population-level effects of complex interactions between individual fish and a spatially and temporally variable stream environment, as first demonstrated by Jager et al. (1993). It also provides a tool for evaluating specific response variables of importance, such as growth and population abundance (Fig. 1). A spatially explicit approach is necessary because of the high spatial variability of stream habitat. We simulated the important mechanisms by which flow and temperature affect individual fish, while otherwise limiting the model's complexity. Existing formulations for such mechanisms were adapted where feasible. The spatial scale chosen (habitat units, divided into longitudinal cells of uniform hydraulic conditions) was limited by the hydraulic modeling technology we adapted from PHABSIM. We selected a daily time step so
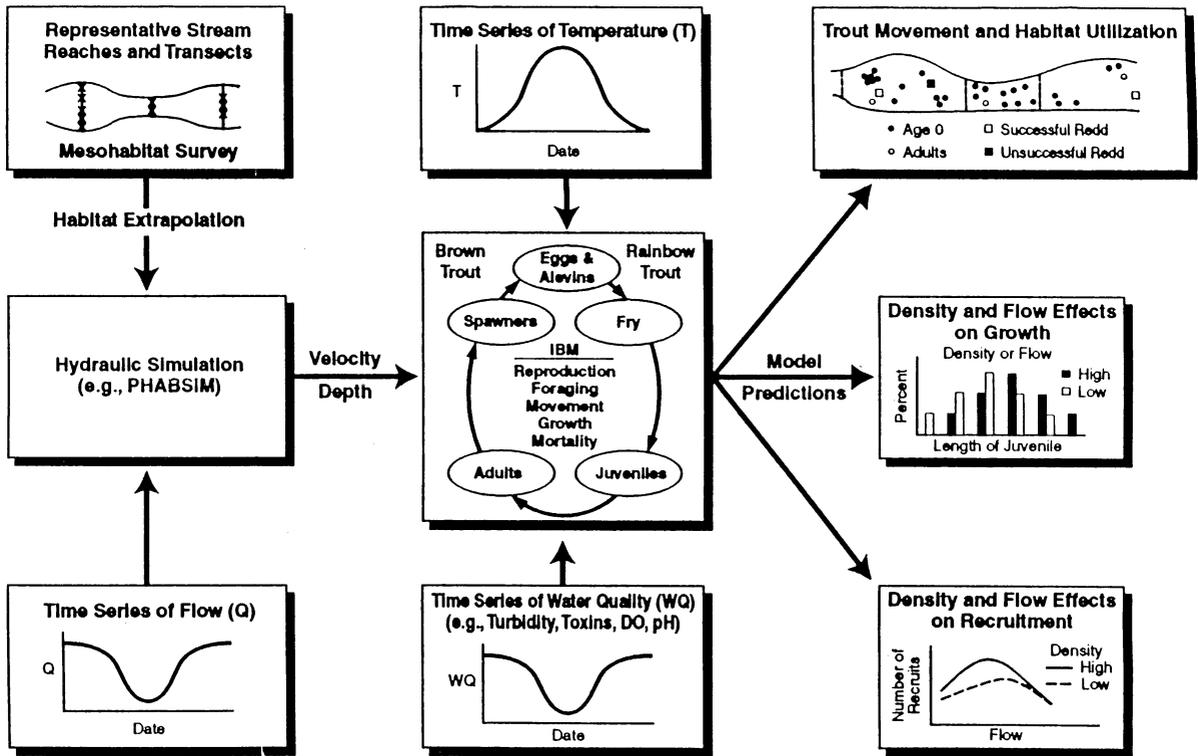
Fig. 1. Schematic of the model for sympatric stream populations of brown and rainbow trout. Individual-based models like the one described in this paper complement and extend IFIM/PHABSIM.

that important effects of short-term events (e.g. flood flows) can be simulated; shorter time steps would require excessive computation. The model is run for multiple consecutive years so that the long-term effects of population-limiting events can be evaluated.

Individual-based models are inherently stochastic. Examples of stochasticity include selecting the direction for a fish to move, selecting the day on which spawning occurs for a given female, and whether an individual fish dies on a given day. Consequently, model results vary stochastically as well as in response to environmental and biological inputs.

The purpose of this paper is to describe the trout model, methods developed to calibrate it, and results of calibration. Reasons for using this type of model in assessing the potential consequences of alternative flow and temperature regimes are discussed.

2. Model description

The model simulates the complete trout life cycle (Fig. 1). The egg stage begins when fertilized eggs are deposited in a redd and ends at hatching. The alevin life stage begins at hatching and ends at emergence from the redd. The model tracks individual redds rather than individual eggs and alevins. On the day of emergence an alevin is reclassified as an age 0 trout, which we assume has no yolk reserves and is capable of feeding; each trout is then followed as an individual. 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 compete for space and prey with brown and native rainbow trout, and their presence may alter predation and fishing effort. The model simulates habitat and trout in a stream segment of any length (typically ≥ 1 km) on a daily time step.

The model description is organized as follows: physical habitat, habitat use and movement, spawning, development and mortality in the redd, growth, and mortality. Parameter values and definitions are listed in Appendix A. Van Winkle et al. (1996) provide a more comprehensive description of the model, although the following description includes modifications to the model made since that report was prepared.

2.1. Physical habitat

Physical habitat complexity is important because it influences the daily and long-term dynamics of fish in streams (Schlosser, 1987; Sedell et al., 1990). Quantifying this complexity from the fish's perspective, however, continues to be a major challenge (Sullivan, 1986; Lamouroux et al., 1995; Sutton and Nestler, 1996). Our model is designed to produce a realistic streamscape of trout habitat (depth, velocity and habitat units) that responds to streamflow (Jager et al., 1997b). 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 growth and mortality of individual trout on an average daily basis and of reproduction and population abundance on an annual and multi-year basis. Achieving this goal involves simplifications and approximations in representing both stream habitat and the biology and ecology of trout. Flow and temperature influence many other stream habitat variables known to be important to fish, such as depth, velocity, prey availability and mortality risks. Average daily temperature and flow are calculated from functions or read in as daily time series. Habitat type (or mesohabitat) refers to the classification of stream habitats at the spatial scale of pools, runs, pocket waters, riffles and cascades (Bisson et al., 1982; Sullivan, 1986; Hawkins et al., 1993). We define 'habitat unit' as a length of stream having a given habitat type.

The model requires two types of information to characterize a stream segment. The first is a mesohabitat map of the entire segment represented in the model. Data for the map ideally include (1) the sequence of habitat types and (2) the length, mean width, mean depth, water surface slope and cover characteristics for each habitat unit at a base or reference flow. The second type of information required is hydraulic data relating depth and velocity to flow at stations along representative, cross-stream transects at two or more flows representing the range of flows of interest. These transects are chosen to represent hydrologically important habitat types (e.g. pool, run, pocket water and riffle).

The model simulates the average water column velocity and depth as a function of flow on a daily basis for cells running the longitudinal length of each pool, run, pocket water and riffle habitat unit. Because it is not feasible to measure the hydraulics of all habitat units in large segments of a stream, we developed a method of simulating the hydraulics of all habitat units from those having PHABSIM transects (Jager et al., 1997b; Van Winkle et al., 1996). In addition to depth and velocity, the model tracks daily changes in the wetted area of each habitat unit. This wetted area (A_{HU}) is used in representing the availability of spawning habitat, feeding station and cover.

Cover is another relevant measure of habitat complexity represented in this model. For each habitat unit in the Tule River, Studley et al. (1995) estimated the fraction of bottom area having instream cover (F_{cov}) at base flow; we assume this fraction applies at all flows. We define an index of cover (A_{cov}, m^2) to represent habitat complexity based on these measurements:

$$A_{cov} = f_{cov} \cdot F_{cov} \cdot A_{HU}, \tag{1}$$

where the wetted area of a habitat unit (A_{HU}) varies with flow, and f_{cov} is a scaling factor. We represent the size-frequency distribution of locations providing cover as an exponential distribution of the 'length' of these locations (L_{cov}), assuming that there are many locations that provide cover for small trout and relatively few locations that provide cover for large trout. The median size (mm) of locations providing cover is specified by L_{covmed}. Access to cover, in turn, is in our formulations for movement, foraging, activity respiration, and risk of predation mortality.

2.2. Habitat use and movement

Trout growth and survival are heavily dependent upon habitat conditions. Trout can move readily, therefore we must simulate how they select among available sites and why they move. In developing formulations for habitat use and movement, we have kept in mind the space and time scales that we can realistically represent in this model. We do not claim to predict the minute-to-minute location of each trout. Rather, a trout is located each day in a cell within a habitat type with specified characteristics (i.e. velocity, depth, cover, density of other trout) as a means of simulating daily average flow-related effects on the energetics, movement, spawning and risks of mortality for that trout.

2.2.1. Access to feeding station and cover

Trout compete for two resources in our model: (1) feeding station and (2) cover as a velocity shelter while foraging. Trout size is assumed to be the primary determinant of dominance used by trout when competing for these resources (Jenkins, 1969). The order of dominance when sizes are equal appears to be brown trout > rainbow trout > hatchery rainbow trout. We quantify these generalities by adjusting the actual length of each model trout with a species-specific dominance factor (v_{spp}), i.e. $L_{dom} = v_{spp} \cdot L$. These adjusted lengths are used to give first access to a feeding station and cover. Trout in a given habitat unit are ranked in decreasing order by L_{dom} value, age 0 brown and rainbow in one group and all older trout in a second group. Values for v_{spp} are adjusted in calibrating the model to match our field observations that a higher fraction of brown than rainbow have feeding station and cover and most hatchery trout do not have these resources.

Feeding station is defined as the area used and defended by a trout while foraging on drift (Grant and Kramer, 1990). We use the regression equation of Grant and Kramer (1990) for station area as a function of fork length, $A_{stat1} = a_{stat} \cdot L^{b_{stat}}$. On each day we rank all trout in a given habitat unit in decreasing order of L_{dom} value, keeping track of the cumulative area of feeding station already assigned. When addition of the station

area required by the next model trout exceeds the station area not already allocated, the less dominant trout does not have access to a feeding station in its current habitat unit on that day and may incur a higher activity respiration cost while feeding and a reduced consumption rate. The total station area (A_{stat2}) of each habitat unit is updated each day as a function of its wetted area (A_{HU}), i.e. $A_{stat2} = c_{stat} \cdot A_{HU}$, where c_{stat} is a scaling factor that is determined during model calibration to ensure that a reasonable percentage of trout for the reference case have feeding stations. This scaling factor has one value for age 0 trout and another value for older trout. Feeding station is not a contested resource at extreme temperatures (T_{min}, T_{max}).

Each trout that obtains feeding station may also have access to cover as a velocity shelter while foraging. The probability of a trout of length L getting a velocity shelter (P_{cov1}) is assumed to follow an exponential distribution, reflecting the exponential distribution of cover availability with locations of cover having a median size of L_{covmed}:

$$P_{cov1} = e^{-L/L_{covmed}}. \tag{2}$$

All cover with length ≥ the length of the trout is initially available. However, each trout assigned a velocity shelter while foraging removes an area of cover equal to the square of its length from the total area of cover still available. Thus, a trout of length L has access to cover as a velocity shelter, only if

$$L^2 \le P_{cov1} \cdot A_{cov} - A_{covas}, \tag{3}$$

where A_{covas} is the cumulative area of cover (m²) already assigned to larger trout on that day. When addition of the area of cover required by the next trout exceeds the area of cover remaining to be allocated in a habitat unit, that trout and less dominant trout in that habitat unit do not have cover as a velocity shelter while foraging on that day.

The probability of access to cover as a refuge from predation (P_{cov2}), as distinct from the probability of access to cover as a velocity shelter while foraging (P_{cov1}), is a function of the area under the length–frequency curve for cover between the

trout's length and that of a potential predator, scaled by the fraction of bottom area having instream cover in a given habitat unit (F_{cov}):

$$P_{cov2} = F_{cov} \cdot [e^{-L/L_{covmed}} - e^{-f_{gape} \cdot L/L_{covmed}}]. \quad (4)$$

The minimum length for a potential predator is determined by f_{gape}, the ratio of the length of the smallest predator that could prey on a given trout to the length of that trout. Cover as a refuge from predation is not treated as a contested resource.

2.2.2. Decision to move and selection of new cell

The model stream segment, as well as a real stream, can be viewed as a two-dimensional surface of mortality risk and growth potential that changes over time in response to changes in flow, temperature, prey availability, competitors and predators. Each trout is 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 previous days. We assume that trout move with the two goals of minimizing mortality risk and maximizing growth, and that they have a sense of mortality risk and growth potential and the capability to assess the tradeoff between them (Werner and Gilliam, 1984). In addition, a low daily probability exists of a trout moving from its current cell for unspecified reasons, P_{move}.

We treat the six risks of mortality (see Section 2.6) as independent probabilities and calculate a daily risk of mortality due to all causes as

$$P_{tot} = 1.0 - \prod_{i=1}^{6} (1.0 - P_i). \quad (5)$$

Daily change in weight is used as an integrated measure of energy intake and energetic costs, and is defined as $\Delta W(t) = [W(t) - W(t-1)]$. A trout's expectation of mortality risk and expectation of daily growth in weight is simulated as a running average of the ratio of its unique history of mortality risks and growth (μ g^{-1} rule), weighted by a memory factor (f_{mem}) (Bernstein et al., 1988, 1991). Each trout may move if, on the previous day, its ratio of mortality risk to growth was greater than expected (Tyler and Rose, 1994). The model is coded to allow selection of the maximizing-growth rule (Hughes, 1998), but the results presented here used the μ g^{-1} rule.

A trout does move if it can locate a cell in its habitat unit or neighboring habitat units. Selection of a cell, like the decision to move, reflects a behavioral strategy of minimizing the risk of mortality by not selecting a cell that is physically uninhabitable because of velocity being too high or depth too shallow (d_{move}), both of which depend on trout length. If no habitable cell is found within the trout's current habitat unit, then adjacent habitat units are evaluated. The direction (upstream or downstream) is chosen at random, although impassable cascades can limit upstream movement, especially of age 0 trout. This formulation allows trout to move out of a unit with uninhabitable water depth and velocity and also allows us to project the change in habitat use with age and size of trout.

2.3. Spawning

The model provides a tool for evaluating the effects of flow, temperature and physical habitat on spawning success. Timing of extreme flow events in relation to spawning activity can be quite different for these two species because they spawn in different seasons. As an example, 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 necessarily affecting the redds of rainbow trout, which spawn later in the spring (Seegrist and Gard, 1972; Moyle, 1976).

In this section we describe our formulations for (1) sexual maturity, and timing and order of spawning, (2) dependence of spawning on flow and physiological condition, (3) selection of a spawning site, (4) superimposition, and (5) fecundity. Energetic costs of reproduction are not considered.

2.3.1. Sexual maturity, and timing and order of spawning

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 primarily a function 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 below). Minimum age at sexual maturity is age 1 for both species and both sexes. For each trout age 1 and older, the probability of sexual maturity is a linear function of length (L_{mat}, L_{spawn}).

Both photoperiod and temperature influence the timing of spawning (Lam, 1988), although brown trout and especially rainbow trout exhibit considerable plasticity in the timing of spawning. We specify start and end dates to the spawning period for each species on a site-specific basis (J_{sp1}, J_{sp2}). 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 species-specific temperature intervals (T_{spmin}, T_{spmax}).

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 for other fish species (e.g. Rose and Cowan, 1993). An algorithm similar to that developed by Rose and Cowan (1993) is used 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 day after the first day the temperature 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 the temperature is greater than or equal to her assigned spawning temperature and there is a warming trend, i.e. $T(t - 1) < T(t)$.

Both brown trout and rainbow trout females may build more than one redd, and spawn on more than 1 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 1 day. 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.

2.3.2. Dependence of spawning on flow and physiological condition

Spawning activity of salmonids can be delayed or disrupted by high flows and by sudden changes in flow. In the model, spawning does not occur if flow exceeds bankfull flow. In addition, conditions for redd construction and spawning are considered unacceptable when the relative change in flow from the previous day exceeds ΔQ. 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}.

2.3.3. Selection of a spawning site

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 calculated as $P_{spawn} = f_{spawn}F_{spawn}$, where a single value of the adjustment factor (f_{spawn}) is determined during model calibration to ensure that nearly all sexually mature trout select a habitat unit for spawning and to control the number of times superimposition (discussed below) occurs. We use estimates at base flow for the fraction of bottom area judged suitable for spawning (F_{spawn}) (Studley et al., 1995). These estimates are based on consideration of substrate (but not velocity and depth) for each habitat unit. For each habitat unit evaluated by a trout, a number is selected at random from a uniform [0, 1] distribution. If the number is less than or equal to the P_{spawn} value for that unit, the trout selects the unit. If the number is greater than P_{spawn}, then the search for a habitat unit continues until one is found (Van Winkle et al., 1996). Once a habitat unit is selected, a cell within that unit is selected as described in Section 2.2. In subsequent years, trout spawn in their natal habitat units.

2.3.4. Superimposition

Superimposition is the construction of one redd on top of an existing redd, 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 (Essington et al., accepted). 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 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 with a distribution characterized by a limited number of larger sites with suitable spawning habitat. Although not considered in the simulations presented in this paper, trout may preferentially select a spawning site where another trout has already constructed a redd (Essington et al., accepted) or where groundwater upwelling occurs (Ottaway et al., 1981; Curry et al., 1994), which would tend to increase the probability of superimposition.

In the absence of quantitative data, but with the above generalities in mind, we estimate the maximum number of non-overlapping sites for redds in a habitat unit as

$$N_{\text{sites}} = f_{\text{spawn}} \cdot F_{\text{spawn}} \cdot \frac{A_{\text{HU}}}{A_{\text{redd}}}. \quad (6)$$

A_{HU} is the wetted area (m^2) of the habitat unit, and A_{redd} is the average area for a redd (m^2) (Ottaway et al., 1981). F_{spawn} and f_{spawn} are defined in the preceding subsection. 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 existing redd is lost.

2.3.5. Fecundity

Fecundity (F, number of mature ova in the ovaries of a female on the day of spawning) is represented as a power function $F = a_{\text{fec}} \cdot L^{b_{\text{fec}}}$ of length (L) on the day of spawning. Considerable phenotypic variability exists among resident stream populations of brown and rainbow trout (McFadden and Cooper, 1964; Elliott, 1984; Avery, 1985; Bromage et al., 1990), and thus site- or region-specific estimates of a_{fec} and b_{fec} are desirable.

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). We multiply the fecundity of each spawning female by f_{eggs} to get the number of fertilized eggs successfully deposited in a redd.

2.4. Development and mortality in the redd

The development and risks of mortality for eggs and alevins differ sufficiently from those for subsequent stages. Thus, we describe our formulations for these non-feeding and relatively well-protected live stages separately. 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 emergence from the redd, and (3) four risks of mortality in the redd.

2.4.1. Female size

Several studies suggest a positive relationship between female size, egg size, alevin size at emergence, and subsequent age 0 trout survival (Bagenal, 1969; Elliott, 1984; Avery, 1985). The relevant finding from these experimental results for this model is that larger females produce larger eggs that result in larger alevins at emergence. We summarize this finding by making the length of age 0 trout at emergence a straight-line function of the length of the female parent.

2.4.2. Development rate and emergence

Brown and rainbow trout differ markedly in the development rate of eggs and alevins. 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, such as predation, but they are less protected from other sources of mortality,
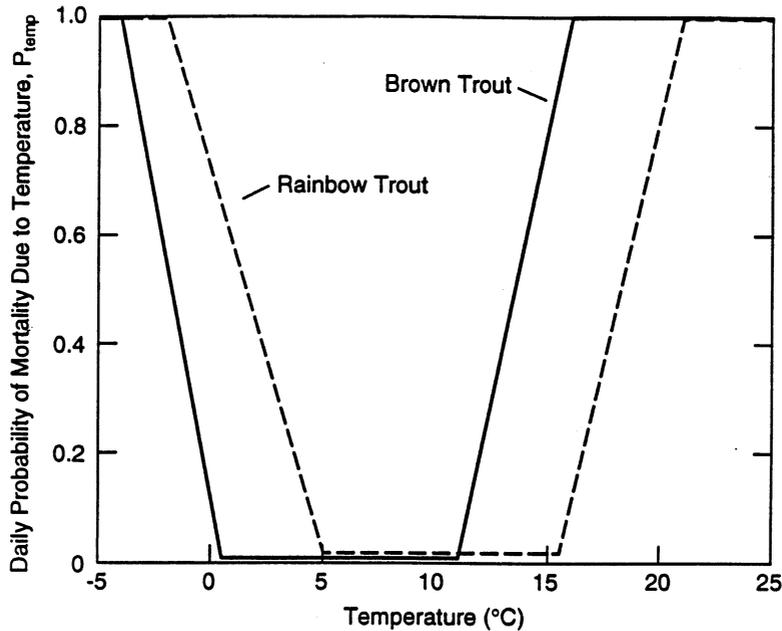
Fig. 2. Daily probability of mortality for eggs and alevins as a function of temperature for brown and rainbow trout.

1987). In addition, some eggs and alevins in the model die each day from unspecified causes. This background mortality risk (P_{bkgd}) is adjusted independently for each species to control the number of age 0 trout that emerge, which facilitates calibrating the model to the observed number of fall age 0 trout.

2.5. Growth

Our growth model links flow, microhabitat and trout behavior to the daily balance between energy acquisition and energetic costs. The formulation describing the daily growth of individual trout is

$$W(t+1) = W(t)$$
$$+ (C - E_{eg} - E_{ex} - E_{SDA} - R) \cdot a_{cal}^{-1},$$
$$(8)$$

where $W(t)$ is the wet weight (g) of a trout on day t, C is energy consumed (cal d^{-1}), and the energy losses (all in cal d^{-1}) are egestion (E_{eg}), excretion (E_{ex}), specific dynamic action (E_{SDA}), and respiration (R) (Hewett and Johnson, 1992). The con-

stant a_{cal} converts calories of trout to grams wet weight of trout.

The model calculates a new weight for each trout on each day. Length is updated based on this weight using a weight–length regression equation, and then a new condition factor is calculated as

$$K(t+1) = \frac{W(t+1)}{a_L \cdot L(t+1)^{b_L}}.$$
$$(9)$$

If the length of a model trout on day t is less than that calculated by using the trout's new weight, the trout's length is increased to that calculated length. Otherwise, $L(t+1) = L(t)$. The maximum value for this condition factor is 1.0; whenever a trout loses weight, its condition factor is < 1.0.

The relative importance of consumption and energy costs for growth of fish in streams is disputed. Some fish ecologists identify consumption as the most uncertain and variable component of growth (Puckett and Dill, 1985; Hughes and Dill, 1990; Hill and Grossman, 1993). Others suggest that activity respiration costs dominate the energetics of stream fishes (Boisclair and Leggett, 1989; Rincon and Lobon-Cervia, 1993).

This model provides a tool for examining the relative importance to growth of food consumption and activity costs.

2.5.1. Consumption

Our model of trout foraging is based on generalizations from the extensive literature on potentially energetically important features of feeding behavior. We treat space (i.e. feeding station and instream cover), rather than prey, as the contested resource. Because fish prey are so seldom found in the stomachs of Tule River trout, this 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; Hughes and Dill, 1990; Hill and Grossman, 1993), who successfully predicted habitat use and growth with simple models relating drift rate, capture efficiency and energetic costs to velocity. The individual-based nature of this model enables us to explore the consequences of different behavioral tactics adopted by individual trout.

Two foraging strategies are commonly observed in nature, the 'sit-and-wait' and the 'active' strategy. Animals using the two strategies show different temporal patterns of energy use while foraging that relate to differences in the rate of energy use during foraging (Goolish, 1992). Both foraging strategies are commonly used by individual brown and rainbow trout and the choice of strategy may be related to social hierarchy, prey availability, access to shelter, and streamflow. Pert and Erman (1994) observed that territorial and transient individuals of a rainbow trout population responded very differently to fluctuating flows. They warn that PHABSIM's use of aggregated habitat curves can conceal important individual differences. Most studies have found that drift feeding and agonistic behavior are more common for trout while holding a feeding station and less common for individuals not associated with a feeding station (Puckett and Dill, 1985; Grant and Noakes, 1987, 1988; Tanida et al., 1989). Trout holding a feeding station had higher consumption rates than those not holding a station in some, but not all, behavioral studies (Grant and Noakes, 1987, 1988).

Our foraging model distinguishes trout that employ a sit-and-wait foraging strategy from those that swim to encounter prey. To do this, we propose several simplifications of reality that reflect current understanding about trout with access to a feeding station ('stayers') and those without ('movers'). We assume that an individual's choice of strategy applies for the daily timestep, although Grant and Noakes (1987) observed that individuals often switched from moving to staying many times during a 15-min observation. Model trout have opportunities to change strategy over a period of days, and thus the penalty imposed by the choice of a daily time step is minor. The opportunity to gain access to a feeding station occurs daily based on trout size (see Section 2.2). Some model trout may forego a feeding station because flow conditions make the mover strategy more profitable.

Our foraging paradigm suggests that drift feeding is most profitable at intermediate velocities. In slow water, the rate of drift delivery approaches zero. In fast water, drift intake is reduced by the decreasing reactive distance of the trout and by its ability to hold position in the water column. This pattern has been observed in several stream fishes, with maximum drift consumption rates at a strike velocity (i.e. water velocity at the point of prey capture) of 7.5 cm·s^{-1} for brook charr (Grant and Noakes, 1987) and 12 cm·s^{-1} for smallmouth bass (Simonson and Swenson, 1990). At a given water velocity, the optimal drift foraging rate increases with both temperature and trout length.

Consumption rate is a product of the rate of prey encounter, the probability of attack, and the probability of capture. Prey encounter rate depends on foraging velocity, the supply of prey, and trout size. The probability of attack (P_{att}) increases with the ratio of prey length to predator length (Dunbrack and Dill, 1983) and therefore decreases for larger trout if prey length is assumed constant. We use an average prey length of 5 mm (Bisson, 1978; Skinner, 1985; Bannon and Ringler, 1986; Hill and Grossman, 1993). The probability of attack declines linearly from 1.0 for small age 0 trout (L_{frymin}) to P_{att1} for larger age 0 trout (L_{att1}). For trout larger than L_{att1}, the probability of attack decreases further according to a logistic function that passes through the point (L_{att2}, P_{att2}) (Fig. 3). Consumption rate for large trout is adequate, even though P_{att} is low, because their prey encounter rate is high.

The probability of capture for drift foragers decreases as water velocity increases (Grant and Noakes, 1987; Godin and Rangeley, 1989; Hughes and Dill, 1990; Hill and Grossman, 1993) and increases with temperature and length of the trout. We used empirical data from experiments by Hill and Grossman (1993) to develop a logistic regression model for the probability of capture as a function of these three variables and the distance between the prey and the trout (Van Winkle et al., 1996). We use the ratio of water velocity to trout length as a variable that reflects the relative water velocity in body lengths per second.

The rate of prey consumption (W_{prey}, g wet weight consumed h^{-1}) is a product of the prey supply rate and the trouts reactive distance. We estimate a threshold reactive distance as the distance at which the probability of capture is 0.9 and assume that prey within this radius are successfully captured if they are attacked (Van Winkle et al., 1996). We assume that the concentration of mid-column drift prey remains constant in response to velocity, leading to a linear increase (with slope m_{drift}) in the prey delivery rate (Fausch, 1984; Statzner et al., 1985; Grant and Noakes, 1987). Adjusting m_{drift} allows

us to calibrate against field data on stomach fullness or trout growth. The model searches the water column for the velocity associated with the highest drift consumption rate, and we assume that this is the strike velocity for the drift-foraging trout (see next subsection). The consumption rate for movers is a fraction (f_{eat}) of the consumption rate they would have obtained if they had a feeding station.

2.5.2. Foraging velocity

Velocities available to a model trout influence its foraging success through the probability of capture and the delivery rate of drifting prey. We specify the range of velocities available to a trout and its optimal choice of foraging behavior. The foraging velocity (V_f) is the average of the velocities experienced during feeding activity. This variable represents a key link between flow, habitat and trout energetics for both stayers and movers. For movers, V_f is a specified fraction of the average water column velocity. For stayers, V_f represents a time-weighted average of the strike velocity and waiting velocity. The strike velocity selected by a drift-feeding model trout maximizes its consumption, subject to two constraints: strike velocity cannot exceed the maximum velocity available in the water column (V_{max}) or the trout's maximum swim speed (S_{max}). We estimate V_{max} using an empirical regression equation (Sullivan, 1986), where different slopes are assigned for different mesohabitat types (S_{slopmn}, S_{slopmx}). We estimate S_{max} as (Brett and Glass, 1973; Stewart, 1980)

$$S_{max} = a_{swim} \cdot W^{b_{swim}} \cdot e^{c_{swim} \cdot T}. \tag{10}$$

The link between foraging velocity and energetic costs is described in Section 2.5.5.

2.5.3. Daily consumption

To simulate the consumption of individual trout on a daily basis, we multiply each trout's hourly consumption rate (W_{prey}, see above) by the time spent foraging (t_f). The daily consumption (W_{eat}, g wet wt of prey d^{-1}) is constrained either (1) by the time available for visual feeding or (2) by the maximum quantity of prey that the trout can digest in a day (C_{max}):
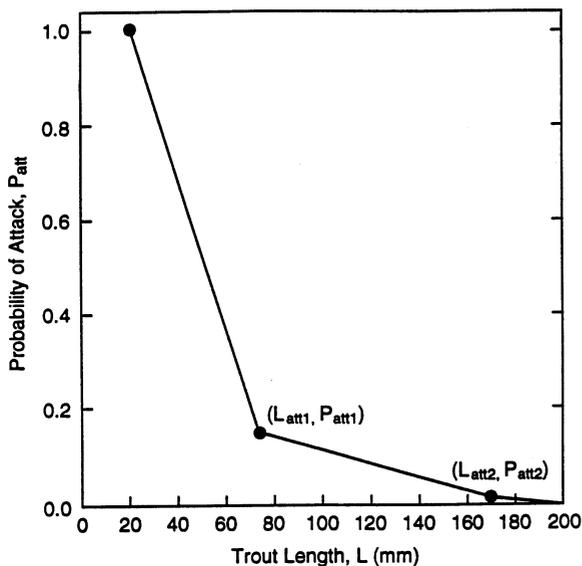

Fig. 3. Two-piece function for the probability that a trout of length L (mm) will attack a 5-mm prey item.

$$W_{eat} = t_f \cdot W_{prey}, \quad W_{eat} < C_{max},$$
$$= C_{max}, \quad W_{eat} \geq C_{max}. \qquad (11)$$

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

Trout are visual foragers (Bachman, 1984). 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. Because trout feed to some extent at night, especially during the hour before sunrise and after sunset, we have modified the formulation of Brock (1981) to include two additional hours of activity every day. The variable t_f in Eq. (12) is the time spent foraging by a trout. If $t_f < t_{actmx}$, it implies that the trout was satiated before being visually limited by low light levels. In practice, W_{prey} is small enough so that t_f generally equals t_{actmx} and realized consumption is less than maximum consumption. Exceptions can occur when the digestion rate is low at extreme temperatures or during periods of high prey abundance (e.g. mayfly hatches). Once the wet weight of prey consumed on a given day has been simulated for an individual trout, this biomass is converted to units of calories of prey consumed on that day (F_{prey}) (Hewett and Johnson, 1992; Rand et al., 1993; Roell and Orth, 1993).

2.5.4. Maximum consumption

When the rate of prey availability exceeds the rate at which trout can digest food, daily consumption is limited by an upper physiological bound. In the model, we represent maximum consumption (C_{max}, g wet wt of prey consumed d^{-1}) as a function of the weight of the trout (W, g wet wt) and temperature (T, °C) (Hewett and Johnson, 1992):

$$C_{max} = a_{C_{max}} \cdot W^{b_{C_{max}}} \cdot f(T). \qquad (12)$$

The value for $a_{C_{max}}$ is estimated in calibrating the model. Our calibration criterion is that maximum weight-specific consumption at optimum temperatures is in the range of 5–15% for age 0 trout and 5–10% for age 1 and older trout (Brett and Groves, 1979). We used a temperature model

Table 1
Equations for foraging, waiting, and resting water velocities (V_{act}, V_{wait}, V_{rest}; cm s^{-1}) and swimming speeds (S_{act}, S_{wait}, S_{rest}; cm s^{-1}) for energetic costs for respiration (R, cal d^{-1}) for stayers (with and without cover as a velocity shelter while foraging) and movers

Foraging strategy	Modifications of general equation[a]
Stayers, w/cover	$V_{act} = V_{opt} \leq (V_{max}, S_{max})$; $S_{act} = 0$; $V_{wait} = S_{wait} = 0$; $V_{rest} = S_{rest} = 0$
Stayers, w/o cover	$V_{act} = V_{opt} \leq (V_{max}, S_{max})$; $S_{act} = 0$; $V_{wait} = V_{act} - dv_{cov}$; $V_f = (t^*_{act} V_{act} + t^*_{wait} V_{wait})/(t_{act} + t_{wait})$; $V_{rest} = S_{rest} = 0$
Movers	$V_{act} = f_v V_{ave}$; $S_{act} = S_{opt}$; $t_{wait} = 0$; $V_{rest} = S_{rest} = 0$

S_{max}, maximum swim speed; S_{opt}, optimum swim speed; V_{max}, maximum velocity in the water column; V_{opt}, velocity in the water column that is optimal for foraging.
[a] General equation: $R = [t_{act} \cdot e^{d_R(V_{act} + S_{act})} + t_{wait} \cdot e^{d_R \cdot (V_{wait} + S_{wait})} + t_{rest} \cdot e^{d_R \cdot (V_{rest} + S_{rest})} + (24 - t_{actmx})] \cdot R_{std}$, where R_{std} is standard respiration $= a_R \cdot W^{b_R} \cdot e^{C_R \cdot T}$.

developed by Thornton and Lessem (1978) to represent $f(T)$. Species differences in the $f(T)$ function result in differences in the consumption of brown and rainbow trout, especially when water temperature exceeds 18°C (Elliott, 1975a,b,c, 1976b for brown trout; From and Rasmussen, 1984 for rainbow trout). We impose an additional, species-specific temperature constraint for all trout of a critical lower temperature threshold (T_{crit}), below which there is no consumption or activity respiration (Elliott, 1976b, 1984).

2.5.5. Energetic costs

We simplify the basic bioenergetics equation Eq. (9) by assuming that energetic costs associated with egestion, excretion and specific dynamic action are a constant fraction ($f_{eg\&ex}$) of energy consumed. Elliott (1976b) observed that these three costs could vary widely as individual components, but tended to sum to $\approx 40\%$ of consumption, leaving $\approx 60\%$ of the energy consumed available for growth and respiration (Brett and Groves, 1979; Ware, 1982).

Daily respiration (R, cal d^{-1}) in the model is formulated as standard respiration (R_{std}) multiplied by a time-weighted sum of factors represent-

ing increased energetic costs associated with different activities (Table 1). Activity respiration is believed to be especially important in streams because of energy expenditure associated with dealing with flowing water (Boisclair and Leggett, 1989; Godin and Rangeley, 1989) and relatively low levels of prey (Cada et al., 1987). Because we are concerned with the energetic consequences of habitat selection in streams, we simulate linkages between activity costs, velocity and cover used as a velocity shelter. Our model differs from bioenergetic models not representing flow in that we simulate a more detailed time-budgeting for respiration costs to provide a linkage between water velocity and trout energetics.

The model partitions the daily period of activity into three time periods: t_{rest} hours resting, t_{wait} hours waiting for prey, and t_{act} hours actively foraging. The sum of these three time periods is the maximum number of hours during which a trout can feed on a given calendar day (t_{actmx}). We assume that each time period is associated with different energetic costs that represent the combined effort of actively swimming and holding position in the current. These different energetic costs represent fundamental differences between trout that adopt a mover versus a stayer foraging strategy and between stayers with and without cover as a velocity shelter while foraging (Table 1). Time resting is calculated as $t_{rest} = t_{actmx} - t_{act} - t_{wait}$; commonly it is zero as described previously.

We assume that movers do not spend any time waiting for drifting prey, and thus $t_{wait} = 0$. A mover feeds actively at its optimum swim speed (S_{opt}; Rand et al., 1993) against an average stream velocity that is a specified fraction (f_v) of the average water column velocity (V_{ave}) (Table 1). Stayers employing a sit-and-wait foraging strategy spend a substantial fraction of time waiting, which we estimate as $t_{wait} = t_{actmx} - t_{act}$. We estimate time actively foraging, which includes capture time and handling time, by assuming 5 s per prey item (Bannon and Ringler, 1986) and by estimating the number of prey items by dividing total daily intake (g) by the average weight of a 5-mm prey item (Smock, 1980). The velocity associated with actively foraging for a stayer is the time-weighted average of strike velocity (V_{act}) and waiting velocity (V_{wait}). Strike velocity is the velocity selected by the drift-feeding trout that maximizes its consumption, subject to constraints of availability as described previously (Section 2.5.2). Waiting velocity is zero for trout with access to cover and greater than zero but less than the strike velocity for trout without access to cover ($V_{act} - dv_{cov}$) (Hill and Grossman, 1993).

2.6. Mortality

Trout face different risks of mortality. For some of these risks, enough is known to represent them in a model with considerable confidence (e.g. high temperature), while for others there is greater uncertainty (e.g. predation). In this section we present formulations for several natural mortality risks and angling mortality. Mortality of stocked trout is calculated to achieve a fixed percentage loss within a specified number of weeks following stocking.

2.6.1. Natural mortality

Each model trout is exposed daily to natural mortality risks that depend on local habitat conditions, such as velocity, depth and cover, and on the trout's attributes, such as physiological condition and length. The following natural mortality risks are represented: (1) high temperature, (2) high and low flows, (3) reproduction, and (4) a combination of predation risk and background risks of mortality.

High temperature can directly result in mortality. We define a daily probability of mortality caused by high temperature that is 0.0 below a temperature threshold (T_{CTM}) and that increases linearly to 1.0 over a specified temperature interval ($T_{CTM} + T_{CTMdel}$). Values for these parameters are species specific and are based on critical thermal maximum values in the literature (Coutant, 1970; Wismer and Christie, 1987; Elliott, 1994).

Floods can wash trout out of a stream reach and thus out of the local population. However, when faced with the risk of being swept downstream, trout tend to move to the bottom and other areas of low velocity (Lobon-Cervia, 1996). In the model, we simulate this risk as a function

of bottom velocity, the trout's maximum swim speed, and its access to cover. If a model trout has access to cover, it is protected from being swept downstream. If a trout does not have access to cover, it is lost if the bottom velocity in the trout's cell exceeds the trout's maximum swim speed, which increases with length and temperature Eq. (10).

The model simulates the risks associated with inhabiting a site that is very shallow. A model trout will attempt to leave its current cell when the depth is less than some fraction (d_{die}) of the trout's length. If the 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 (P_{strand}).

Brown trout tend to be longer-lived than rainbow trout in streams (Moyle, 1976; Studley et al., 1995), suggesting that mortality associated with reproduction may be higher for rainbow than brown trout. We assign a one-time risk of mortality to each model trout that reproduces (P_{repro}). In calibrating the model, species-specific values for this risk are determined to help achieve the field densities of adult brown and rainbow trout observed the following fall.

The final risk of natural mortality represented in the model includes consideration of the length and condition of the trout, the time it is active, and whether it has access to cover as a refuge. We distinguish between risks present primarily when a trout is active (e.g. predation) and those always present (e.g. disease). We assume that these mortality risks increase with decreasing condition and size. The daily probability of mortality (P_{mort}) due to predation and these unquantifiable 'background' risks of mortality is:

$$P_{mort} = 1.0 - e^{-z}, \qquad K_{min} < K \leq 1.0,$$

where

$$Z = F_K \cdot F_L \cdot \left[Z_{24} + \left(\frac{t_f}{24} \right) \cdot Z_{act} \right]. \tag{13}$$

The variable Z, the total instantaneous daily mortality rate (d^{-1}), is the sum of mortality rates for those risks always present (Z_{24}) and those present

only during activity (Z_{act}). These two rates are defined for small trout in good condition. The condition-dependent factor (F_K) increases with decreasing condition, and the length-dependent factor (F_L, Fig. 4) increases with decreasing length (Van Winkle et al., 1997b). The Z_{act} term simulates mortality during the fraction of a day a model trout is active, and is zero if the trout has access to cover as a refuge. The baseline value for Z_{act} and the species-specific values for the maximum length parameter (L_{max}) in the length-dependent factor are selected in calibrating the model to observed abundances.

2.6.2. Angling mortality

We represent losses caused by angling in considerable detail for four reasons: it can be a major source of mortality, creel data are commonly available to guide an appropriate formulation, angling mortality is potentially density dependent, and this is one source of mortality that managers can directly influence. We modify a maximum daily probability of angling mortality (P_{fmax}) with a series of independent fractions. The daily probability of angling mortality is

$$P_{angling} = f_{day} \cdot f_{month} \cdot f_{spp} \cdot$$
$$[f_{keep} + (1.0 - f_{keep}) \cdot f_{hook}] \cdot f_{dens} \cdot P_{fmax}. \tag{14}$$

The creel-census data for the Tule River (Studley et al., 1995) indicate that angling mortality is
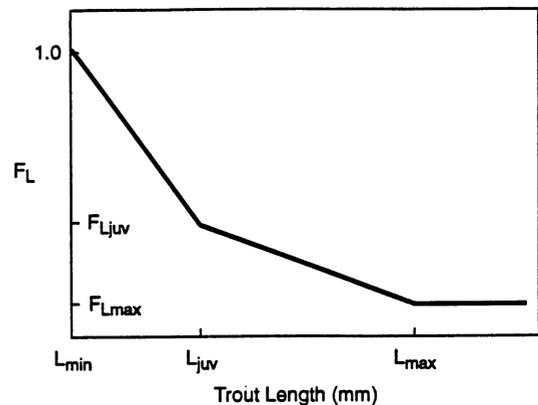

Fig. 4. Length-dependent factor in the equation for the daily probability of mortality due to predation and unquantifiable background risks of mortality (Eq. (13)).
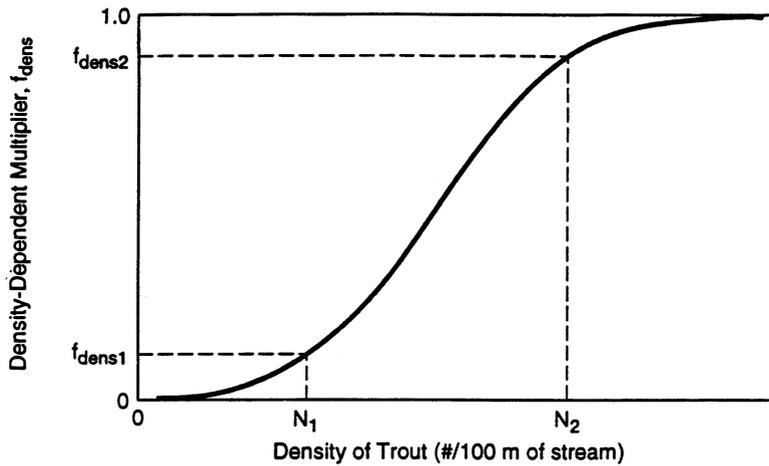
Fig. 5. Density-dependent multiplier of angling mortality as a function of the combined densities of brown, rainbow, and hatchery rainbow trout (Eq. (14)).

higher on weekends than weekdays (f_{day}) and is higher during June than the other five months of the fishing season (f_{month}). Comparing the proportions of brown, rainbow, and hatchery rainbow trout caught to the relative densities of these three groups in the stream indicates that hatchery trout are much more vulnerable than brown or rainbow trout (f_{spp}). The probability that a caught trout is kept (f_{keep}) is greatest for large trout ($L = L_{large}$) and decreases for smaller trout. Released trout experience a small risk of hooking mortality (f_{hook}). The density-dependent factor (f_{dens}) is an increasing logistic function as trout density increases (Fig. 5). The history of stocking hatchery trout in the United States and other countries indicates that fishing effort and mortality increase when stocking occurs (Vincent, 1987; Moring, 1993). We assume that it is legal to catch any age 1 and older wild trout and all hatchery trout, and that anglers respond to their combined density. The model updates density daily to include new stocking of hatchery trout and mortality of trout during the preceding day. Eq. (15) reflects the types of data available for the Tule River (Studley et al., 1995). The approach, however, is easily modified for other sites based on available data and can be used to evaluate the effects of alternative fishing regulations. In calibrating the model to match the creel data, we set f_{spp} for hatchery trout at 1.0 and adjust the f_{spp}

values for brown and rainbow trout and the P_{fmax} value.

2.6.3. Mortality of stocked trout

Most hatchery rainbow trout survive for only 1–2 weeks after stocking (Moyle, 1976; Studley et al., 1995). We assume that the risks of mortality that apply to all trout are independent of each other (i.e. they are competing sources of mortality). Hatchery trout that survive these risks are subjected to an additional daily risk of natural mortality that is selected during model calibration to result in > 90% of hatchery trout dying within 2 weeks of stocking (P_{HRT}).

3. Sensitivity analysis

A sensitivity analysis of a simulation model such as ours is crucial prior to its use as a tool in facilitating management decisions concerning natural resources (Bart, 1995). Such an analysis is also important in guiding model calibration, helping design monitoring and experimental studies, and interpreting the results of such studies. We used the PRISM software package (Gardner et al., 1981; Jager et al., 1997a; Van Winkle et al., 1997b). PRISM draws a latin-hypercube sample of parameter values from a multivariate Gaussian

distribution with specified mean values and a coefficient of variation of 1%. This variation is not intended to represent our uncertainty in the parameters, but only to estimate the influence of varying the parameters near one point in parameter space. The sample vector of parameter values is transformed to ensure near-independence among parameters. The sensitivity analysis ranked model parameters by their effect on six model response variables at the end of 1-year simulations. These six variables, for each of the two species, were length of age 0, 1 and 2 trout; abundance of age 0, 1 and older trout; and number of eggs spawned.

Results of the sensitivity analysis indicated that there was relatively little overlap in the parameters that most influenced growth versus abundance. Growth for brown and rainbow trout of all ages, as indexed by length at the end of 1-year simulations, was most sensitive to the following parameters: (1) average supply rate of drifting prey (m_{drift}), (2) two parameters that reduced intake for older, larger trout (P_{att1} and L_{att2}; Fig. 3); (3) the exponent of the function for the area of a trout's feeding station as a function of trout length (b_{terr}); (4) the intercept parameter in the equation for probability of capture (a_{rd}); and (5) the three parameters defining the dependence of standard respiration on body weight and water temperature, especially the exponent on weight (b_R) (Table 1 and Appendix A). Variability in these parameters accounted for 20–90% of the variability in growth, depending on the species and age class. As noted by others in sensitivity analyses of bioenergetics models (Bartell et al., 1986; Beauchamp et al., 1989), parameters related to energy intake (i.e. consumption), rather than energetic costs, account for most of the variability in growth.

Number of eggs spawned and abundance of age 0 for both species were most sensitive to the exponent of the function for fecundity as a function of female length (b_{fec}). Survival of these eggs and alevins was also sensitive to the background mortality in the redd (P_{bkgd}). Survival of the subsequent age 0 trout was most sensitive to the daily instantaneous mortality rate for those risks present when a trout is active (Z_{act}). Survival of

age 1 and older trout of both species, as indexed by abundance at the end of 1-year simulations, was also most sensitive to Z_{act}, and to parameters in the length-dependent factor of the function for the daily probability of mortality due to predation and unquantified background risks of mortality (Fig. 4). Although these were the most sensitive parameters, variability in these parameters accounted for < 50% of the variability in number of eggs spawned and abundance for both species and all three age classes.

4. Model calibration

Bart (1995) and Rykiel (1996) proposed several criteria for the calibration of an individual-based simulation model that should be satisfied prior to using the model to address management and assessment issues. One of Bart's criteria is that model predictions and field observations should be in reasonable agreement. We calibrated our trout model, using both 1-year and multi-year simulations and 9 years of field observations from the North Fork Middle Fork Tule River, Tulare County, California.

4.1. Site-specific conditions

Input and calibration data were available for the North Fork Middle Fork Tule River, Tulare County, California, from a long-term study by Pacific Gas & Electric Corporation (PG&E) (Studley et al., 1995). The study segment we selected for calibration is ≈ 1.1 km long at an elevation of 1160–1220 m. It extends from Tule River Diversion Dam to Doyle Springs Diversion Dam. Both dams are effective barriers to upstream movement at all flows and to downstream movement at low flows, but not at flows high enough to result in spills. Flow in this stream segment is partially controlled by the Tule River Diversion Dam, which has a diversion capacity of ≈ 1.9 m^3 s^{-1}; natural flows above 1.9 m^3 s^{-1} spill at the Tule River Diversion Dam. There is very little storage capacity created by Doyle Springs Diversion Dam; consequently, when water spills at the Tule River Diversion Dam, water also spills
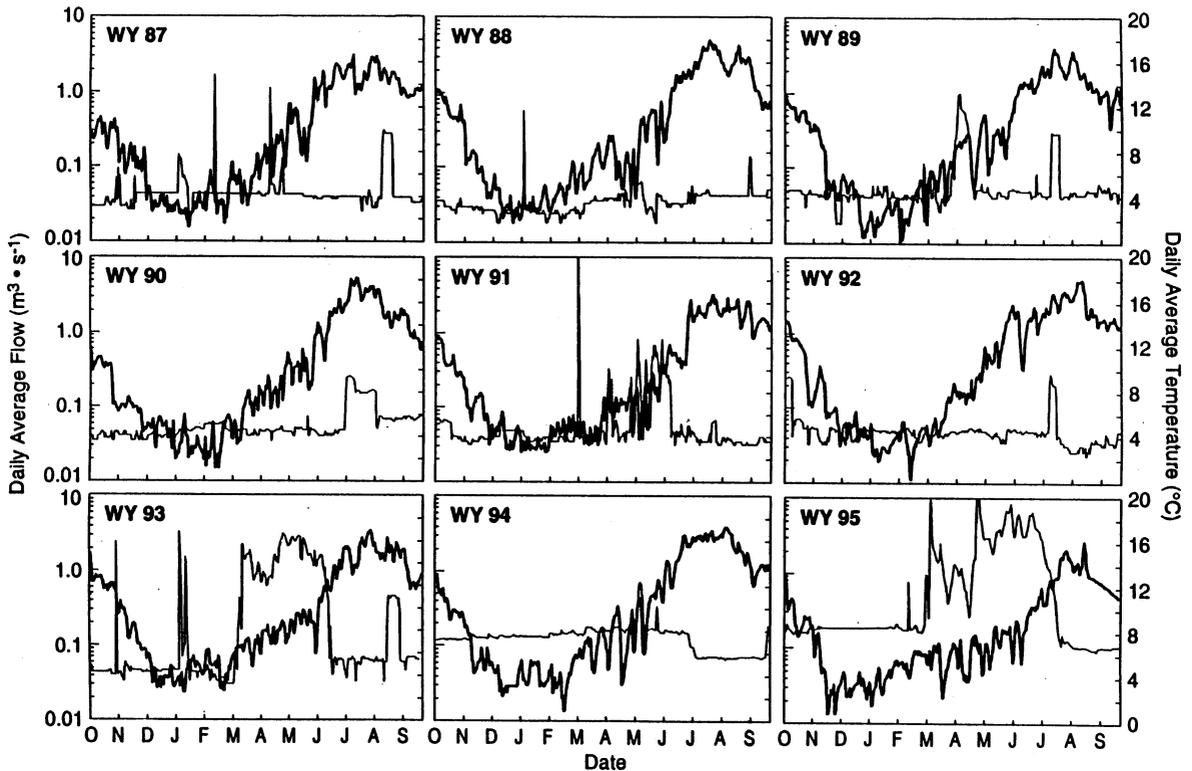
Fig. 6. Daily mean stream flow (light line) and temperature (heavy line) recorded below Tule River Diversion Dam for water years 1987–1995. The daily mean flow on March 4, 1991, was 12.6 m^3 s^{-1}; the extremely high hourly maximum flow exceeded 34 m^3 s^{-1}, and was used in model simulations.

at Doyle Springs Diversion Dam. Fifty percent exceedance flows above Tule River Diversion range from 0.34 m^3 s^{-1} in September to 3.96 m^3 s^{-1} in May. Fifty percent exceedance flows below Tule River Diversion range from 0.031 m^3 s^{-1} in January to 1.76 m^3 s^{-1} in May. Stream flows were relatively low during the drought water years (Fig. 6; WY87–WY91), although a maximum hourly flow of > 34 m^3 s^{-1} occurred on March 4, 1991 (Fig. 6; WY91). Water years 1993 and especially 1995 were relatively wet years, while water year 1994 was a relatively dry year. PG&E altered the minimum flows in this segment starting in summer 1993 as follows: 0.142 m^3 s^{-1}, October 1 to June 30; 0.051 m^3 s^{-1}, July 1 to September 30. Prior to summer 1993, PG&E voluntarily released a minimum flow of ≈ 0.042 m^3 s^{-1}.

The study segment included two 100-m electrofishing stations. Fish population data used in

this paper were collected at these stations from fall 1986 to fall 1995. Macrohabitats in this stream segment consisted primarily of pools and pocket water. Mean width and depth at 0.031 m^3 s^{-1} was 4.5 m and 38.9 cm, respectively. Mean maximum pool depth was 80.5 cm. Cobble and rubble were the dominant substrates. Percentage cover averaged 13%, and percentage spawning habitat averaged 2.6%.

Fish species present include wild rainbow and brown trout, and hatchery rainbow trout. Rainbow trout are dominant in numbers, but brown trout are dominant in biomass. The great majority of hatchery rainbow trout usually disappear within 2 weeks of being planted, and they are not known to survive through the winter. The California Department of Fish and Game planted between 2268–10 147 rainbow trout per year (1987–1992) between April and September. Wild
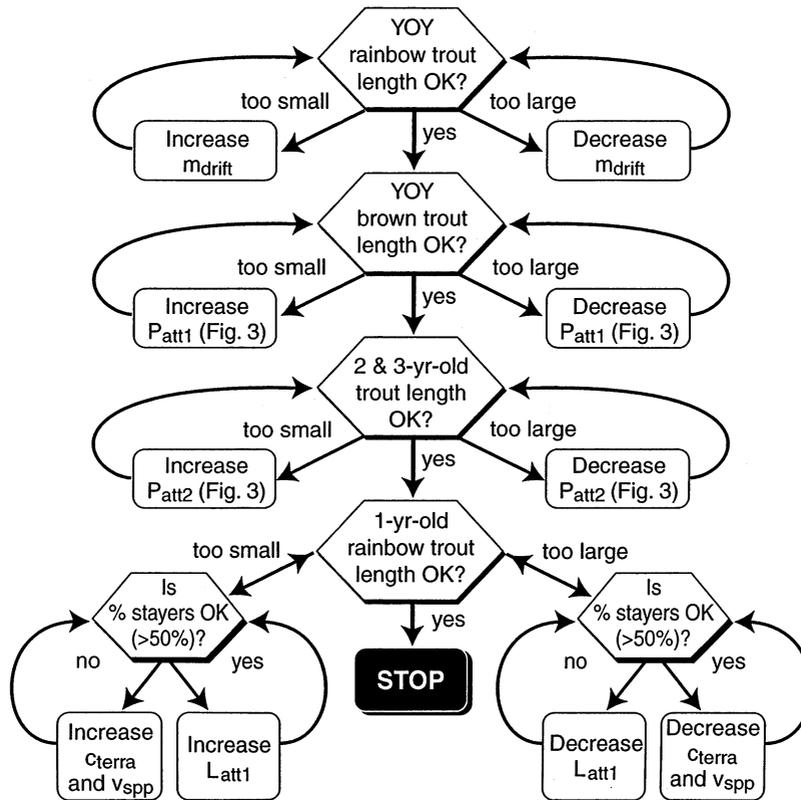
Fig. 7. Calibration procedures for growth.

rainbow trout spawn successfully every year, but brown trout redds are occasionally subjected to high flows in winter months that greatly reduce the incoming year class. Winter temperatures and ice are not considered limiting to trout. Summer stream temperatures are < 20°C and are not considered limiting to trout.

We define the initial number, age composition, and length and weight distributions of brown and rainbow trout populations in the model on October 1 of each water year, as measured in fall population surveys (Studley et al., 1995; T.K. Studley, PG&E, personal communication). The initial length of each model trout is selected at random from a symmetric triangular distribution with a mode equal to the average measured length for that age and species. The weight (W) of each trout is then selected at random from a triangular distribution with a mode equal to the weight calculated from the species-specific regression equation

$$W = a_L \cdot L^{b_L}. \tag{15}$$

The sex ratio for age 1 and older trout is assumed to be 1:1. On the first day of each simulation, age 1 and older trout are assigned in equal density to all pool habitat units, and age 0 trout are assigned in equal density to all pool, run, pocket water, and riffle habitat units. Hatchery rainbow trout are assigned to several large pool habitat units at weekly intervals during the stocking season to approximate actual stocking locations and rates (Studley et al., 1995; Van Winkle et al., 1996). Daily flow and temperature regimes for water years 1987–1995 are given in Fig. 6.

4.2. Calibration procedure

We first calibrate the model for length of ages 0, 1 and 2 of each species at the end of 1-year simulations (i.e. September 30 of the following year). These predictions reflect the outcome of
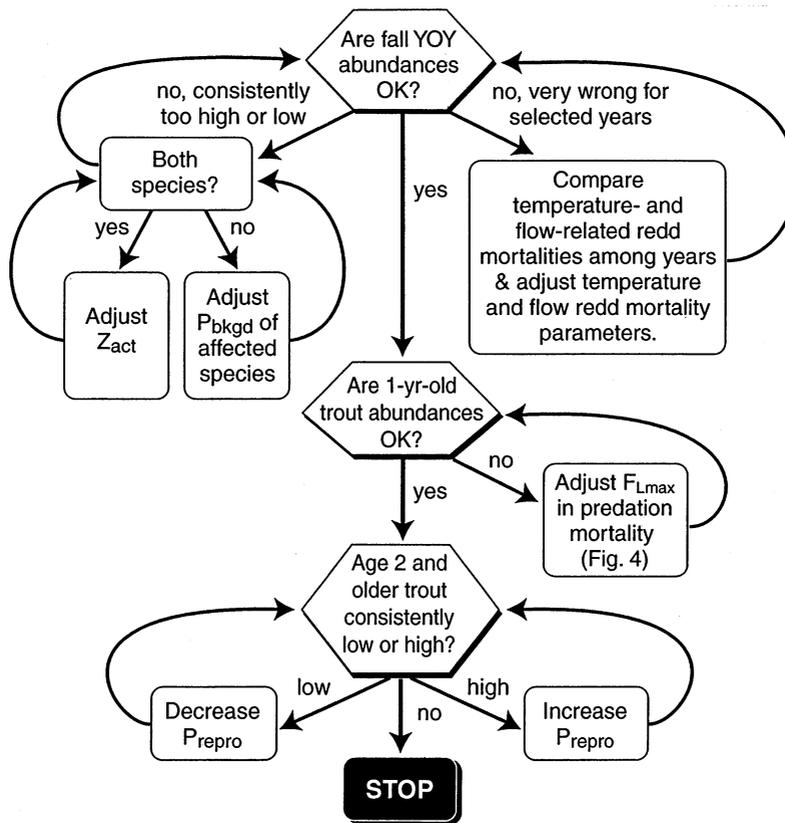
Fig. 8. Calibration procedures for survival.

many events and integrate bioenergetic processes throughout the year. We developed a flow chart for varying the most sensitive parameters controlling the balance between energy intake and energetic costs (Fig. 7). Based on results of our sensitivity analysis indicating that simulated growth is more sensitive to key parameters influencing energy intake than energetic costs (Section 3) and based on the lack of information on prey availability, we focus on energy intake when calibrating the model.

We calibrate the model for abundance of age 0 trout of each species and then for the abundance of trout age 1 and older of each species. We developed a flow chart for varying the most sensitive parameters controlling the mortality rates of the different life stages (Fig. 8). The abundance of age 0 brown and rainbow trout at the end of 1-year simulations reflects the number and size of

females that spawn, when they spawn, the flow and temperature regimes during incubation, timing of emergence, and mortality of age 0 trout from emergence until September 30.

Little is known quantitatively about the relative importance of the different mortality risks that reduce the abundance of age 1 and older trout in the Tule River (or other streams) or about the mechanisms whereby the abundance of one species is influenced by the abundance of the other. Although we represent several mortality risks for age 1 and older trout (Section 2.6), values for the parameters in these formulations are not well-grounded on empirical data. In addition, because movement of trout into and out of the study segment was not monitored (Studley et al., 1995), we have assumed that the net balance between immigration and emigration is zero for all life stages of both species.

We calibrated the model to achieve the best agreement possible between observed and predicted lengths and abundances for each of the two species for 9 water years with a single set of parameter values (see Appendix A). Once this set of parameter values was determined, six replicate 1-year simulations, differing only in the initial random number seed, were run for each of the 9 water years. The variability among these replicates reflects the effect of the stochastic events included in the model. As a further calibration test, we ran the model for 50 years to evaluate the stability of model projections of length and abundance. For these 50-year simulations, daily

flow and temperature regimes were selected at random from the 9 years for each of the 50 years. The initial brown and rainbow trout lengths and abundances were those for the water year randomly selected for the first year of the simulation.

Austen et al. (1994) and Studley et al. (1996) make a convincing case for applying the guild concept when considering population abundance and weighted useable area (WUA) for sympatric species that would be expected to respond to environmental change in a similar manner. In other words, "it may be more reasonable to assume that the combined abundance of all species in a guild can more accurately reflect changes in their primary resource or a limiting factor" (Austen et al., 1994). With this concept in mind, and although the model was calibrated to give the best simultaneous fit to brown trout age 1 and older, and rainbow trout age 1 and older, we compared simulated and observed values for abundance of total trout age 1 and older.

4.3. Calibration results

Predicted and observed lengths on September 30 for each of the 9 water years are in reasonable agreement for all three ages of both species (Fig. 9). The average of the 54 year-by-year absolute percentage differences between predicted and observed length is $\approx 5\%$. The maximum percentage difference for brown trout is $+17\%$ for age 0 in 1995 (13 mm too large). The maximum percentage difference for rainbow trout is $+17\%$ for age 1 in 1994 (21 mm too large).

The coefficients of variation (CV) for predicted length for the six replicate 1-year simulations for each of the 9 water years were $< 6\%$ for all three ages of both species, except for brown trout age 0 in 1991 (CV = 20%). This relatively high CV for brown trout age 0 reflects the stochastic formulations in the model in combination with the effects of the major flood event on March 4, 1991, in scouring brown trout redds. Because of the low variability in predicted length for replicate simulations, and in spite of the reasonable agreement between predicted and observed lengths (Fig. 9), the average predicted length $\pm$ two standard deviations includes the observed length in only 23 of the 54 cases.
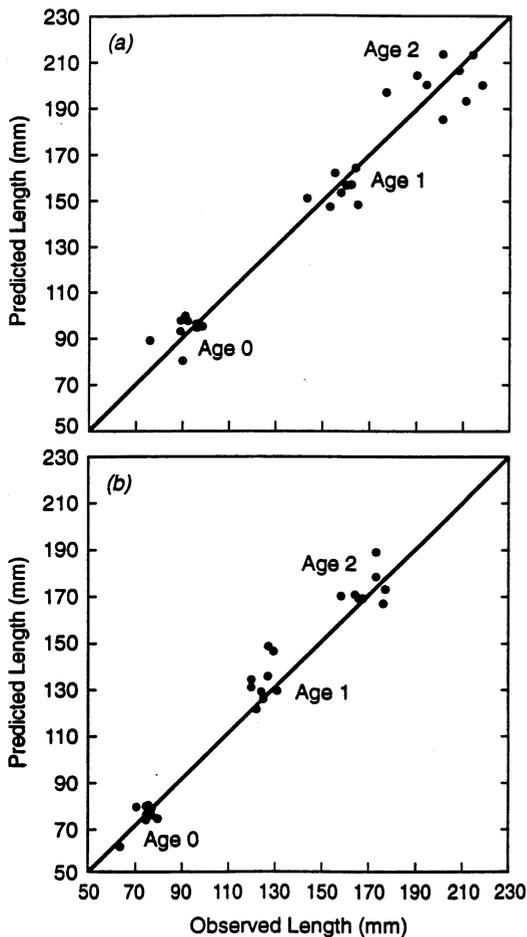

Fig. 9. Comparison of predicted and observed length on September 30 from 1-year simulations for 9 water years (1987–1995) for (a) brown trout ages 0, 1 and 2, and (b) rainbow trout ages 0, 1 and 2. The diagonal is the 1:1 line for predicted and observed values.
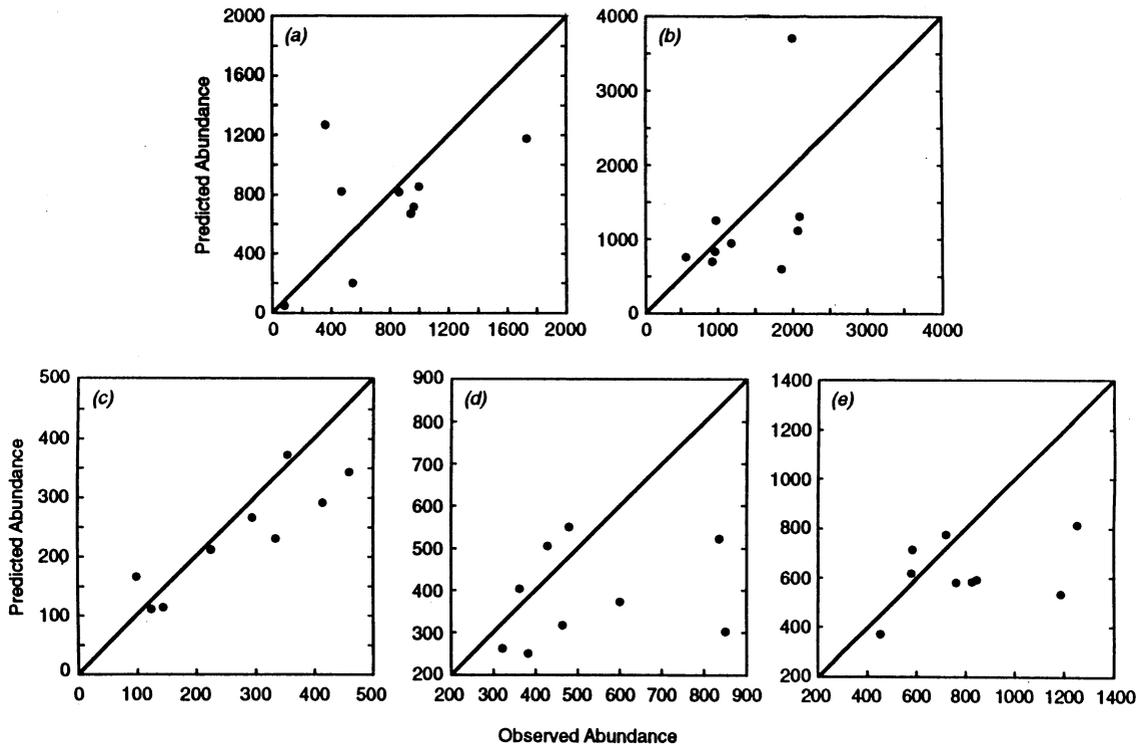
Fig. 10. Comparison of predicted and observed abundance on September 30 from 1-year simulations for 9 water years (1987–1995) for (a) age 0 brown trout, (b) age 0 rainbow trout, (c) age 1 and older brown trout, (d) age 1 and older rainbow trout, and (e) age 1 and older total trout. The diagonal is the 1:1 line for predicted and observed values.

Predicted and observed abundances on September 30 for each of the 9 water years for age 0 and for age 1 and older trout demonstrate greater differences than for lengths and are greater for age 0 than age 1 and older (Fig. 10). The average of the nine absolute percentage differences is 60% for age 0 brown trout (Fig. 10(a)), 40% for age 0 rainbow trout (Fig. 10(b)), 23% for age 1 and older brown trout (Fig. 10(c)), 30% for age 1 and older rainbow trout (Fig. 10(d)), and 25% for age 1 and older total trout (Fig. 10(e)).

The CVs for predicted abundance for the six replicate 1-year simulations for each of the 9 water years were, on average, greater than for predicted length, and were more variable for age 0 than age 1 and older. For example, CVs were < 20% for age 1 and older brown and rainbow trout for all water years, except 1989 when CV ≈ 40% for both species. The CVs for age 0 brown and rainbow trout, however, exceeded 20% in

nine of 18 cases and was at a maximum (61%) for age 0 brown trout in the flood year of 1991. Differences in CVs by age and species reflect differences in the outcomes of stochastic events during these 1-year simulations, which have a greater effect on predicted abundances than predicted lengths. As was the case in comparing predicted and observed lengths, the average predicted abundance ± two standard deviations includes the observed abundance in approximately half of the 45 comparisons (Fig. 10).

Results from a 50-year simulation indicate that simulated lengths for age 0 and age 1 rainbow trout and simulated abundances for age 1 and older rainbow trout are stationary over the long term (Fig. 11). As expected, the year-to-year fluctuations are greater for abundance than length, and for this simulation there is a suggestion of a cycle in abundance primarily due to the chance selection of a sequence of water years relatively
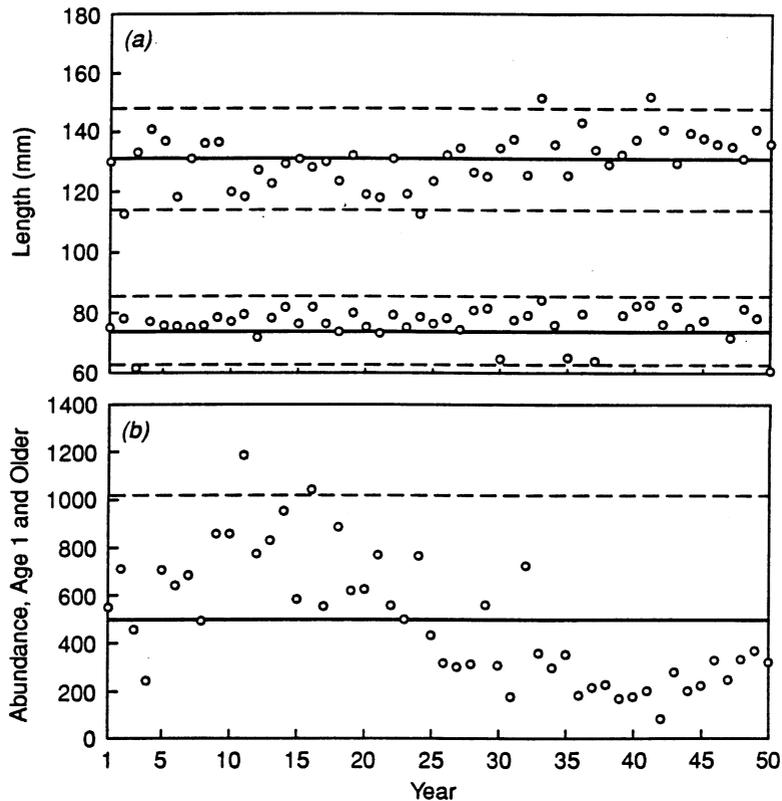
Fig. 11. Examples of projected abundance and average length on September 30 for each of 50 years: (a) length of age 0 and age 1 rainbow trout, and (b) abundance of age 1 and older rainbow trout. The solid horizontal lines are the average abundance or length projected for the 50 years; the dashed horizontal lines indicate ± 2 S.D. about this average.

unfavorable for rainbow trout. A major component of the yearly variability in abundance is a function of the frequency and magnitude of winter and spring floods that scour brown or rainbow trout redds. These flood events have a multi-year effect in that the resulting small age 0 year classes of brown trout advance to become small age 1 and then age 2 cohorts in following years.

5. Discussion

The model described in this paper provides a tool for projecting flow and temperature effects on trout populations by linking the hydraulic component of IFIM/PHABSIM to an individual-based population model (Fig. 1). Based on a sensitivity analysis and expert opinion, the model was calibrated for a stream segment in the Tule River, California. The calibration results indicate that our coupling of an individual-based bioenergetics model with a simulation of stream physical habitat, under a variety of flow and temperature regimes but using a single set of parameter values, can provide (a) predictions of trout growth over 1 year that are in good agreement with field data, (b) predictions of changes in trout abundance over 1 year that are not in as good agreement with field data, and (c) long-term projections of both length and abundance that are stationary.

Simulating growth involves our bioenergetics formulations for consumption and energetic costs. These formulations are dependent, in part, on our dynamic representation of the physical habitat (depth, velocity and cover) involving PHABSIM

and habitat mapping data. The formulations and many of the parameters in these formulations are more strongly based on experimental and field measurements than is the case for mortality. Causes, numbers, locations, and timing of mortalities in the field are rarely known. In addition, the net effect of migration in and out of the study segment is unknown in this case and was assumed to be zero in the simulation model. Finally, the field data for length indicate limited inter-annual variability, whereas the field data for abundance indicate considerable inter-annual variability. Consequently, as found in this study, predicting growth more accurately than abundance is to be expected.

One reason for developing this model was to link PHABSIM-based data on 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. 1). Habitat suitability indices are required in PHABSIM applications to estimate weighted usable area (WUA). Several studies have demonstrated, however, that the results of such applications are more sensitive to habitat suitability indices than representation of physical habitat (Mathur et al., 1985; Orth, 1987; Armour and Taylor, 1991; EA Engineering, Science and Technology, 1994). Castleberry et al. (1996) and Van Winkle et al. (1997a) have recently discussed uncertainty and instream flow standards and the need to pursue additional approaches. The response of fish populations to altered flows project and other studies have documented that factors in addition to those involved in an IFIM/PHABSIM analysis can limit trout populations (Orth, 1987; Lewis et al., 1994; Studley et al., 1995, 1996). Substitution of an individual-based population model in place of habitat suitability indices increases realism by mechanistically representing the processes underlying the reproduction, growth and survival of individuals as they pass through their life cycle.

Variability and uncertainty in both field data and replicate model simulations are realities that have implications for scientists, resource managers, and regulators in projecting growth and abundance responses to alternative flow or temperature regimes. Field data on length and abundance by age class collected at two similar sites on the same day under similar temperature and flow conditions may vary for several reasons, generally unknown and unquantifiable. For example, the Tule River length and abundance data we used to calibrate this model are the average of data from electrofishing samples at two similar, 100-m sites. The CVs for yearly differences between these two similar sites in fall abundance estimates for 1987–1992 are: 75% for brown trout age 0; 255% for rainbow trout age 0; 72% for brown trout age 1 and older; 82% for rainbow trout age 1 and older; and 216% for total trout age 1 and older. The CVs for differences in length estimates between the two sites exceeded 100% for all ages of both species. This type of variability and uncertainty in both field data and simulation model results emphasizes the importance of maintaining realistic expectations concerning the ability of simulation models to make accurate predictions, as opposed to improving understanding (Dale and Van Winkle, 1998).

This is a stochastic simulation model. Thus, predictions of length and abundance by age class from replicate model simulations, that differ only in the random number seed, are different due to the effects of stochastic events. These events are all known and their individual contributions to variability can be quantified. Stochastic phenomena in the model include the following: initial lengths and weights of trout; risks of mortality; spawning temperature assigned to mature females; movement; and events related to reproduction. Stochasticity has been included for these events to represent both the actual stochasticity of events in the field and our uncertainty concerning these phenomena (Strange et al., 1992). Although the bioenergetics formulations depend on depth and velocity, which varies with location, the equations determining growth are deterministic. Thus, it is not surprising that in 50-year simulations the relative inter-annual variability in length is low ($< 10\%$) compared with that for abundance.

Simulation models of the type presented here are potentially valuable tools for assessing the likely effects of alternative instream flow and temperature regimes. Although the price of increasing realism is increasing complexity (Ney, 1993), this modeling approach is now at a stage of development where evaluation of this tradeoff between realism and complexity is needed. This model represents one in a series of tools designed to incrementally improve methods for instream flow evaluations. Seven reasons for using such models, especially in assessments where the financial stakes are high, are as follows:

(1) The link between changes in habitat and population are explicit, which provides a framework for designing site-specific monitoring programs of habitat and fish populations.

(2) There are limiting factors other than WUA that can affect the populations response to changes in flow that are represented in the trout model but that cannot be explicitly represented using the IFIM/PHABSIM approach. These include food availability, temperature effects, inter- and intra-species competition, and scouring flows (Orth, 1987). For example, the sublethal effects of temperature are considered. These are neglected when temperature is managed using temperature criteria such as a maximum temperature of 20°C for trout.

(3) Models of this type predict measurable and relevant endpoints, such as fish length and abundance, as well as intermediate responses such as stomach fullness and habitat utilization. Such endpoints are of direct value in monitoring and adaptive management studies.

(4) The daily time step allows realistically synthesized temperature and flow data to be used. Real flow releases and temperatures are more variable than those typically assumed in assessments, and actual flows are often significantly different from the regulatory minimum releases that are assumed in IFIM/PHABSIM studies.

(5) The time series effects of population-limiting events are simulated when multi-year runs are used. An example is scouring of brown trout redds during high winter flow events. The effect of scouring is subsequently reflected as reduced brown trout abundance for that year class for several years and (perhaps) by a compensatory increase in rainbow trout abundance (Strange et al., 1992).

(6) Density-dependent effects are included. This could be important for examining effects of limited spawning habitat, limited adult habitat, high angling mortality, and entrainment losses in water diversions.

(7) Model projections are valuable for identifying stream management options that are more likely than other options to minimize adverse effects on fish populations.

Acknowledgements

Appendix A. Input parameters (as of 7/18/97)

Name, value, definition and reference for model parameters are listed in alphabetical order under the same headings used in the text: physical habitat, habitat use and movement, spawning, development and mortality in the redd, growth, and mortality. The absence of a reference for a parameter means that the value for that parameter is our best estimate based on evaluation of the literature, the values for related parameters, and results of calibrating the model.

Parameter name	Parameter value[a]	Definition and reference
Physical habitat		
f_{cov}	0.01	Adjustment factor for fraction of the area of a habitat unit with cover
L_{covmed}	150	Median length (mm) of locations providing cover
S_{slopmn}, S_{slopmx}	0.00, 0.01; 0.02, 0.06; 0.02, 0.06; 0.01, 0.02	(Minimum, maximum) water surface slope for pool, riffle, pocket water, and run habitat units, respectively (Sullivan, 1986)
Habitat use and movement		
a_{stat}, b_{stat}	3.55E-6, 2.45	Parameters for area of a trout's feeding station as a function of trout length (Grant and Kramer, 1990)
c_{staty}, c_{stata}	0.05 (age 0), 0.15 ($\geq$age 1)	Adjustment factors for feeding station available in a habitat unit for Age 0 and for older trout, respectively; value determined in calibrating for the baseline simulation
d_{move}	1.5	Multiple of a trout's length required for a cell to be habitable in terms of depth
f_{pred}	2.5	Ratio of (length of smallest predator that could prey on a given trout)/(length of that trout)
f_{mem}	0.5	Daily memory factor used in calculating a trout's expectation of mortality risk and energetic status, which in turn influences movement (Tyler and Rose, 1994)
P_{move}	0.01	Probability of a trout moving from its current cell because of unspecified reasons (i.e. stochastic movement or exploratory behavior)
T_{min}, T_{max}	BT: 6.0, 19.0; RT: 8.0, 21.0	Minimum and maximum temperature (°C), respectively, below which and above which feeding station is not a contested resource (Campbell and Neuner, 1985; Heggenes et al., 1993; Riehle and Griffith, 1993)
v_{spp}	BT: 1.0; RT: 0.8; HRT: 0.1	Weighting factor for species used in dominance ranking of trout for access to feeding station and cover as a velocity shelter
Spawning		
A_{redd}	0.3	Average area of a redd (m²) (Ottaway et al., 1981)
a_{fec}, b_{fec}	BT: 1.16, 2.54; RT: 1.16, 2.54	Parameters of the equation for fecundity as a function of female length (Avery, 1985)
f_{eggs}	0.9	Fraction of the number of mature eggs produced by a female that are successfully fertilized and deposited in a redd (McFadden and Cooper, 1964)
f_{lost}	0.5	Fraction of eggs and alevins lost from an existing redd because of each occurrence of superimposition
f_{spawn}	10	Adjustment factor for fraction of the area of a habitat unit suitable for spawning

J_{sp1}, J_{sp2}	BT: Oct 1–Dec 31; RT: Mar 15–Jul 31	Calendar dates for the start and end of the spawning season (Moyle, 1976)
K_{sp}	0.75	Minimum condition factor on day of spawning required for spawning
L_{mat}, L_{spawn}	BT: 170, 210; RT: 140, 170	Lengths (mm) defining the straight line for probability of sexual maturity from 0 to 1.0
ΔQ	0.1	Threshold for fractional change in daily flow above which a female delays spawning until a later day
T_{spmin}, T_{spmax}	BT: 4.0, 10.0; RT: 8.0, 13.0	Minimum and maximum temperature (°C), respectively, for spawning (Moyle, 1976; Elliott, 1984; Wismer and Christie, 1987; Billard, 1992)

Development and mortality in the redd

a_{dev}, b_{dev}, c_{dev}	BT: 3.13E-3, 3.07E-5, 9.34E-5; RT: −2.54E-4, 1.34E-3, 3.21E-5	Parameters for daily development rate of eggs and alevins as a quadratic function of temperature (Embody, 1934; Elliott, 1984)
A_{redd}	0.3	Average area of a redd (m^2) (Ottaway et al., 1981)
D_{dewat}	0.0	Water depth (m) at which a redd is dewatered
L_{mat}, L_{fry1}; L, L_{fry2}	BT: 170, 20; 300, 30; RT: 140, 20; 220, 30	Coordinates of the two points defining the straight line relating length of fry at emergence (mm) to length of female parent (mm)
P_{bkgd}	BT: 0.009; RT: 0.018	Daily risk of mortality of eggs and alevins caused by unspecified, density-independent sources of mortality
P_{dewat}	0.4	Daily risk of mortality for eggs and alevins because of dewatering of the cell in which the redd is located
T_1, T_2, T_3, T_4	BT: −4.0, 0.5, 11.0, 16.0; RT: −2.0, 5.0, 15.5, 21.0	Temperature parameters (°C) for daily risk of mortality as a function of temperature for eggs and alevins; see Fig. 2
V_{bott1}, V_{bott2}	0.7, 1.6	Bottom water column velocities (m·s^{-1}) in a logistic function for daily risk of mortality for eggs and alevins because of scouring, corresponding to a risk of 0.01 and 0.95, respectively

Growth

a_{cal}	1400, 1000	Conversion factor (cal·g^{-1}) between calories and grams wet weight for age 1 and older trout and for age 0 trout, respectively (Hewett and Johnson, 1992)
a_{Cmax}, b_{Cmax}	0.60, 0.76	Parameters for maximum consumption as a function of weight
a_L, b_L	BT: 0.0000132, 2.97; RT: 0.0000147, 2.96	Parameters for wet weight (g) of a trout as a function of its length (mm FL)
a_R, b_R, c_R	7.13, 0.780, 0.0693	Parameters for standard respiration as a function of weight and temperature; see Table 1
a_{rd}, b_{rd}, c_{rd}, d_{rd}	5.91, 0.847, 0.0473, 1.74	Parameters for probability of capture as a logistic function of relative water velocity, temperature, and distance between prey and the trout (Hill and Grossman, 1993; Van Winkle et al., 1996)
a_{swim}, b_{swim}, c_{swim}	44.1, 0.128, 0.0405	Parameters for maximum swim speed as a function of trout weight and temperature

d_{swim}, e_{swim}, f_{swim}	2.84, 0.485, 0.0405; 9.70, 0.128, 0.0405	Parameters for optimum swim speed as a function of the trout weight and temperature. The first set is for trout >150 g wet weight; the second set is for trout >150 g wet weight (Stewart, 1980; Rand et al., 1993; Van Winkle et al., 1996); see Table 1
d_R	0.030	Parameter for activity respiration as a function of water velocity or swimming speed; see Table 1
dv_{cov}	5.6	Difference between strike and waiting velocity for trout without access to cover (cm s^{-1}) (Hill and Grossman, 1993); see Table 1
f_{eat}	0.80	Fraction of the consumption rate for movers relative to what they would have obtained as a stayer
$f_{eg\&exy}$, $f_{eg\&exa}$	0.40, 0.40	Proportion of energy consumed that is lost because of egestion, excretion, and specific dynamic action for age 0 trout and for older trout, respectively (Brett and Groves, 1979)
f_v	0.80	Water velocity used by movers as a fraction of average water column velocity in that cell
$f(T)$	BT: T, °C RT: T, °C $f(T)$ $f(T)$	Temperature-dependent function multiplying weight-dependent maximum consumption (Thornton and Lessem, 1978)
	7.0 0.20 4.0 0.20 15.0 0.70 15.0 0.70 18.0 0.98 22.0 0.98 20.0 0.20 24.0 0.20	
F_{prey}	600	Conversion factor between grams wet weight and calories for invertebrate prey (Hewett and Johnson, 1992)
$(L_{frymin}, 1.0)$; (L_{att1}, P_{att1}); (L_{att2}, P_{att2})	(20, 1.0); (75, 0.144); (170, 0.01)	(X-axis, Y-axis) coordinates for the three points specifying the two-piece function for the probability that a trout of length L (mm) will attack a 5-mm prey item (Dunbrack and Dill, 1983); see Fig. 3
m_{drift}	0.000010	Slope of straight line for water velocity versus drift rate (cal h^{-1} cm^{-2}) (Fausch, 1984, Fig. 2)
T_{crit}	3.0	Critical lower temperature (°C) for foraging and activity respiration
Mortality		
d_{die}	0.25	Minimum depth as a fraction of a trout's length; used in representing the probability of stranding
f_{day}	Mon–Thu: 0.85; Fri–Sun: 1.0	Adjustment factor for angling mortality for weekdays and for weekends and holidays
f_{hook}	0.1	Adjustment factor for angling mortality for hook & release
f_{keep}, L_{large}	0.8, 300	Probability of keeping a caught trout of length = L_{large} (mm). This probability decreases linearly with slope L/L_{large} for smaller trout
f_{month}	Apr: 0.2; May: 0.8; Jun: 1.0; Jul: 0.8; Aug: 0.6; Sep: 0.2; Oct–Mar: 0.0	Adjustment factor for angling mortality by month

f_{spp}	BT: 0.05; RT: 0.10; HRT: 1.0	Adjustment factor for angling mortality for differences in catchability between species
K_{min}	0.75	Minimum condition factor required for survival
$(L_{min}, 1.0)$; (L_{juv}, F_{ljuv}); (L_{max}, F_{Lmax})	BT: (20, 1.0); (25, 0.333); (300, 0.010); RT: (20, 1.0); (25, 0.333); (240, 0.010)	(X-axis, Y-axis) coordinates for the three points specifying the piece-wise, straight-line function in the length-dependent factor for P_{mort}; see Fig. 4
(N_1, f_{dens1}); (N_2, f_{dens2})	(100, 0.20); (200, 0.95)	(X-axis, Y-axis) coordinates for the two points specifying the logistic function for the density-dependent factor in the equation for angling mortality; see Fig. 5
P_{fmax}	0.04	Maximum daily probability of angling mortality
P_{repro}	BT: 0.40; RT: 0.90	Risk of mortality because of reproduction
P_{strand}	0.5	Daily probability of mortality because of being stranded
P_{HRT}	0.152	Expected daily probability of mortality for hatchery rainbow trout
T_{CTM0}, T_{CTM1}	BT: 26.0, 26.0; RT: 26.0, 26.0	Temperature (°C) above which the daily probability of mortality due to high temperature starts to increase from 0.0 to 1.0 for age 0 and for age 1 and older, respectively
T_{CTMdel}	2.0	Temperature increment (°C), added to T_{CTM0} (and T_{CTM1}), specifying the temperature interval over which the daily probability of dying due to high temperature increases from 0.0 to 1.0
Z_{act}	0.018	Daily instantaneous mortality rate for those risks present primarily when a trout is active
Z_{24}	0.0025	Daily instantaneous mortality rate in the P_{mort} function for those background risks present 24 h day^{-1}

[a] BT, brown trout; RT, rainbow trout; HRT, hatchery rainbow trout. When no species is indicated, parameter values relating to trout apply to all species.

References

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, 36 pp.

Armour, C.L., Taylor, J.G., 1991. Evaluation of the instream flow incremental methodology by U.S. fish and wildlife service field users. Fisheries 16 (5), 36–43.

Austen, D.J., Bayley, P.B., Menzel, B.W., 1994. Importance of the guild concept to fisheries research and management. Fisheries 19 (6), 12–20.

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, 13 pp.

Bachman, R.A., 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Trans Am. Fish. Soc. 113, 1–36.

Bagenal, T.B., 1969. Relationship between egg size and fry survival in brown trout *Salmo trutta* L. J. Fish. Biol. 1, 349–353.

Bannon, E., Ringler, N.H., 1986. Optimal prey size for stream resident brown trout (*Salmo trutta*): tests of predictive models. Can. J. Zool. 64, 704–713.

Bart, J., 1995. Acceptance criteria for using individual-based models to make management decisions. Ecol. Appl. 5 (2), 411–420.

Bartell, S.M., Breck, J.E., Gardner, R.H., Brenkert, A.L., 1986. Individual parameter perturbation and error analysis of fish bioenergetics models. Can. J. Fish. Aquat. Sci. 43, 160–168.

Beauchamp, D.A., Stewart, D.J., Thomas, G.L., 1989. Corroboration of a bioenergetics model for sockeye salmon. Trans. Am. Fish. Soc. 118, 597–607.

Bernstein, C., Kacelnik, A., Krebs, J.R., 1988. Individual decisions and the distribution of predators in a patch environment. J. Anim. Ecol. 57, 1007–1026.

Bernstein, C., Kacelnik, A., Krebs, J.R., 1991. Individual decisions and the distribution of predators in a patch environment. II. The influence of travel costs and structure of the environment. J. Anim. Ecol. 60, 205–225.

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. J. Fish. Res. Bd. Can. 35, 971–975.

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

Boisclair, D., Leggett, W.C., 1989. The importance of activity in bioenergetics models applied to actively foraging fishes. Can. J. Fish. Aqat. Sci. 46, 859–1967.

Bovee, K.D., 1982. A guide to stream analysis using the instream flow incremental methodology. Instream Flow Information Paper No. 12. FWS/OBS 82/26. U.S. Fish and Wildlife Service.

Brett, J.R., Glass, N.R., 1973. Metabolic rates and critical swimming speeds of sockeye salmon (Oncorhynchus nerka) in relation to size and temperature. J. Fish. Res. Bd. Can. 30, 379–387.

Brett, J.R., Groves, T.D.D., 1979. Physiological energetics. In: Hoar, W.S., Randall, D.J., Brett, J.R. (Eds.), Fish Physiology, Volume VIII, Bioenergetics and Growth. Academic Press, New York, pp. 280–352.

Brock, T.D., 1981. Calculating solar radiation for ecological studies. Ecol. Model. 14, 1–19.

Bromage, N., Hardiman, P., Jones, J., Springate, J., Bye, V., 1990. Fecundity, egg size and total egg volume differences in 12 stocks of rainbow trout, Oncorhynchus mykiss Richardson. Aquac. Fish. Manag. 21, 269–284.

Cada, G.F., Loar, J.M., Sale, M.J., 1987. Evidence of food limitation of rainbow and brown trout in southern Appalachian soft-water streams. Trans. Am. Fish. Soc. 116, 692–702.

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

Castleberry, D.T., Cech, J.J. Jr., Erman, D.C., Hankin, D., Healey, M., Kondolf, G.M., Mangel, M., Mohr, M., Moyle, P.B., Nielsen, J., Speed, T.P., Williams, J.G., 1996. Uncertainty and instream flow standards. Fisheries 21 (8), 20–21.

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, WA.

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

Dale, V.H., Van Winkle, W., 1998. Models provide understanding, not belief. Bulletin of the Ecological Society of America, in press.

DeAngelis, D.L., Gross, L.J., 1992. Individual-based Models and Approaches in Ecology: Populations, Communities, and Ecosystems. Chapman & Hall, New York.

Dunbrack, R.L., Dill, L.M., 1983. A model of size dependent surface feeding in a stream dwelling salmonid. Environ. Biol. Fish. 8, 203–216.

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, 35 pp.

Elliott, J.M., 1975a. Weight of food and time required to satiate brown trout, Salmo trutta L. Freshw. Biol. 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. Freshw. Biol. 5, 287–303.

Elliott, J.M., 1975c. The growth rate of brown trout (Salmo trutta L.) fed on maximum rations. J. Anim. Ecol. 44, 805–821.

Elliott, J.M., 1976a. The downstream drifting of eggs of brown trout, Salmo trutta L. J. Fish. Biol. 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. J. Anim. Ecol. 45, 923–948.

Elliott, J.M., 1984. Numerical changes and population regulation in young migratory trout Salmo trutta in a lake district stream, 1966–83. J. Anim. Ecol. 53, 327–350.

Elliott, J.M.,1994. Quantitative Ecology and the Brown Trout. Oxford University Press, New York, 286 pp.

Embody, G.C., 1934. Relation of temperature to the incubation periods of eggs of four species of trout. Trans. Am. Fish. Soc. 64, 281–292.

Essington, T.E., Sorensen, P.W., Paron, D.G. Behavioral basis, density dependence, and ecological significance of redd superimposition in sympatric salmonids. Can. J. Fish. Aquat. Sci., accepted.

Fausch, K.D., 1984. Profitable stream positions for salmonids: Relating specific growth rate to net energy gain. Can. J. Zool. 62, 441–451.

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

Gardner, R.H., O'Neill, R.V., Mankin, J.B., Carney, J.H., 1981. Comparison of sensitivity analysis and error analysis based on a stream ecosystem model. Ecol. Model. 12, 173–190.

Godin, J.-G.J., Rangeley, R.W., 1989. Living in the fast lane: effects of cost of locomotion on foraging behaviour in juvenile Atlantic salmon. Anim. Behav. 37, 943–954.

Goolish, E.M., 1992. Integrating two views of foraging. Oikos 65, 545–549.

Grant, J.W.A., Kramer, D.L., 1990. Station size as a predictor of the upper limit to population density of juvenile salmonids in streams. Can. J. Fish. Aquat. Sci. 47, 1724–1737.

Grant, J.W.A., Noakes, D.L.G., 1987. Movers and stayers: foraging tactics of young-of-the-year brook charr, *Salvelinus fontinalis*. J. Anim. Ecol. 56, 1001–1013.

Grant, J.W.A., Noakes, D.L.G., 1988. Aggressiveness and foraging mode of young-of-the-year brook charr, *Salvelinus fontinalis* (Pisces, Salmonidae). Behav. Ecol. Sociobiol. 22, 435–445.

Hawkins, C.P., et al., 1993. A hierarchical approach to classifying stream habitat features. Fisheries 18 (6), 3–12.

Heggenes, J., Krog, O.M.W., Lindas, O.R., Dokk, J.G., Bremnes, T., 1993. Homeostatic behavioural responses in a changing environment: brown trout (*Salmo trutta*) become nocturnal during winter. J. Anim. Ecol. 62, 295–308.

Hewett, S.W., Johnson, B.L., 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, 79 pp.

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

Hughes, N.F., 1998. A model of habitat selection by drift-feeding stream salmonids at different scales. Ecology 79, 281–294.

Hughes, N.F., Dill, L.M., 1990. Position choice by drift-feeding salmonids: model and test for arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. Can. J. Fish. Aquat. Sci. 47, 2039–2048.

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

Jager, H.I., Cardwell, H.E., Sale, M.J., Bevelhimer, M.S., Coutant, C.C., Van Winkle, W., 1997a. Modelling the linkages between flow management and salmon recruitment in rivers. Ecol. Model. 103, 171–191.

Jager, H.I., Van Winkle, W., Holcomb, B.D., Railsback, S.F., 1997b. Will hydrologic climate changes in Sierra-Nevada streams influence trout persistence? Trans. Am. Fish. Soc. (accepted).

Jenkins, T.M., 1969. Social structure, position choice and micro-distribution of two trout species (*Salmo trutta* and *Salmo gairdneri*) resident in mountain streams. Anim. Behav. Monogr. 2, 56–123.

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

Lamouroux, N., Souchon, Y., Herouin, E., 1995. Predicting velocity frequency distributions in stream reaches. Water Res. 31, 2367–2375.

Lewis, A.F., Mitchell, A.C., Prewitt, C.M., 1994. Evaluation of the effectiveness of water release as a mitigation to protect fish habitat. Report 9118 G 878. Prepared for Canadian Electrical Association, Montreal, Quebec, by Triton Environmental Consultants LTD, Richmond, B.C., and E.A. Engineering Science and Technology, Redmond, WA 98052.

Lobon-Cervia, J., 1996. Response of a stream fish assemblage to a severe spate in Northern Spain. Trans. Am. Fish. Soc. 125, 913–919.

Mathur, D., Bason, W.H., Purdy, E.J., Silver, C.A., 1985. A critique of the instream flow incremental methodology. Can. J. Fish. Aquat. Sci. 42, 825–831.

McFadden, J.T., Cooper, E.L., 1964. Population dynamics of brown trout in different environments. Physiol. Zool. XXXVII, 355–363.

Milhous, R.T., Updike, M.A., Schneider, D.M., 1989. Physical habitat simulation system reference manual—version II. Instream Flow Information Paper 26. 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 Am. J. Fish. Manag. 13, 234–237.

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

Murray, C.B., McPhail, J.D., 1988. Effect of incubation temperature on the development of five species of Pacific salmon (*Oncorhynchus*) embryos and alevins. Can. J. Zool. 66, 266–273.

Ney, J.J., 1993. Bioenergetics modeling today: growing pains on the cutting edge. Trans. Am. Fish. Soc. 122, 736–748.

Orth, D.J., 1987. Ecological considerations in the development and application of instream flow-habitat models. Regul. Rivers 1, 171–181.

Ottaway, E.M., Carling, P.A., Clarke, A., Reader, N.A., 1981. Observations on the structure of brown trout, *Salmo trutta* Linnaeus, redds. J. Fish. Biol. 19, 593–607.

Pert, E.J., Erman, D.C., 1994. Habitat use by adult rainbow trout under moderate artificial fluctuations in flow. Trans. Am. Fish. Soc. 123, 913–923.

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

Rand, P.S., Stewart, D.J., Seelbach, P.W., Jones, M.L., Wedge, L.R., 1993. Modeling steelhead population energetics in Lakes Michigan and Ontario. Trans. Am. Fish. Soc. 122, 977–1001.

Riehle, M.D., Griffith, J.S., 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. Can. J. Fish. Aquat. Sci. 50, 2119–2128.

Rincon, P.A., Lobon-Cervia, J., 1993. Microhabitat use by stream-resident brown trout: bioenergetic consequences. Trans. Am. Fish. Soc. 122, 575–587.

Roell, M.J., Orth, D.J., 1993. Trophic basis of production of stream-dwelling smallmouth bass, rock bass, and flathead catfish in relation to invertebrate bait harvest. Trans. Am. Fish. Soc. 122, 46–62.

Rose, K.A., Cowan, J.H. Jr., 1993. Individual-based model of young-of-the-year striped bass population dynamics. I. Model description and line simulations. Trans. Am. Fish. Soc. 122, 415–438.

Rykiel, E.J. Jr., 1996. Testing ecological models: the meaning of validation. Ecol. Model. 90, 229–244.

Schlosser, I.J., 1987. A conceptual framework for fish communities in small warmwater streams. In: Matthews, W.J., Heins, D.C. (Eds.), The Ecology and Evolution of North American Stream Fishes. University of Oklahoma Press, Norman, Oklahoma, pp. 17–24.

Scott, D.P., 1962. Effect of food quantity on fecundity of rainbow trout, (*Salmo gairdneri*). J. Fish. Res. Bd. Can. 19, 715–731.

Scott, W.B., Crossman, E.J., 1973. Freshwater fishes of Canada. Bulletin 184, Fisheries Research Board of Canada, Ottawa, 966 pp.

Sedell, J.R., Reeves, G.H., Hauer, F.R., Stanford, J.A., Hawkins, C.P., 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. Environ. Manag. 14, 711–724.

Seegrist, D.W., Gard, R., 1972. Effects of floods on trout in Sagehen Creek, California. Trans. Am. Fish. Soc. 101, 478–482.

Simonson, T.D., Swenson, W.A., 1990. Critical stream velocities for young-of-year smallmouth bass in relation to habitat use. Trans. Am. Fish. Soc. 119, 902–909.

Skinner, W.D., 1985. Size selection of food by cutthroat trout, *Salmo clarki*, in an Idaho stream. Gt. Basin Nat. 45, 327–331.

Smock, L.A., 1980. Relationships between body size and biomass of aquatic insects. Freshw. Biol. 10, 375–383.

Stalnaker, C.B., 1993. Fish habitat evaluation models in environmental assessments. In: Hildebrand, S.G., Cannon, J.B. (Eds.), Environmental Analysis. Lewis, Ann Arbor, Michigan, pp. 140–162.

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

Stewart, D.J., 1980. Salmonid predators and their forage in Lake Michigan: A bioenergetics-modeling synthesis. Ph.D. Thesis, University of Wisconsin, Madison, WI, 224 pp.

Strange, E.M., Moyle, P.B., Foin, T.C., 1992. Interactions between stochastic and deterministic processes in stream fish community assembly. Environ. Biol. Fishes 36, 1–15.

Studley, T.K., Baldrige, J.E., Wise, L.M., Spina, A.P., Railsback, S.F., McElravy, E., Travanti, L., Yuen, T.D.F., Lindahl, R.B., Chase, S.D., Smith R.W., 1995. Response of fish populations to altered flows project, Volumes I–III: predicting trout populations from streamflow and habitat variables. Pacific Gas and Electric Company, Report 009.4–94.3, San Ramon, CA.

Studley, T.K., Baldrige, J.E., Railsback, S.F., 1996. Predicting fish population response to instream flows. Hydro. Rev. 15 (6), 48–57.

Sullivan, K., 1986. Hydraulics and fish habitat in relation to channel morphology. Ph.D. Thesis, The Johns Hopkins University, Baltimore, 409 pp.

Sutton, V.K., Nestler, J., 1996. Methods for describing in-channel habitat features: engineering processes to fractal geometry concept. In: LeClerc, M., Capra, H., Valentin, S., Boudreault, A., Cote, Y. (Eds.), Ecohydraulics 2000, Proceedings of the 2nd International Symposium on Habitat Hydraulics, Institut National de la Recherche Scientifique, Quebec, Canada, vol. B, pp. 263–274.

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

Thornton, K.W., Lessem, A.S., 1978. A temperature algorithm for modifying biological rates. Trans. Am. Fish. Soc. 107, 284–287.

Tyler, J.A., Rose, K.A., 1994. Individual variability and spatial heterogeneity in fish population models. Rev. Fish Biol. Fish. 4, 91–123.

Van Winkle, W., Rose, K.A., Chambers, R.C., 1993. Individual-based approach to fish population dynamics: an overview. Trans. Am. Fish. Soc. 122, 397–403.

Van Winkle, W., Jager, H.I., Holcomb, B.D., 1996. An Individual-Based Instream Flow Model for Coexisting Populations of Brown and Rainbow Trout. TR-106258, Electric Power Research Institute, Palo Alto, California, 205 pp.

Van Winkle, W., Coutant, C.C., Jager, H.I., Mattice, J.S., Orth, D.J., Otto, R.G., Railsback, S.F., Sale, M.J., 1997a. Uncertainty and instream flow standards: perspectives based on research and assessment experience. Fisheries 22 (7), 21–22.

Van Winkle, W., Rose, K.A., Shuter, B.J., Jager, H.I., Holcomb, B.D., 1997b. Effects of climate temperature change on growth, survival, and reproduction of rainbow trout: predictions from a simulation model. Can. J. Fish Aquat. Sci, 54, 000–000 (in press).

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 Am. J. Fish. Manag. 7, 91–105.

Ware, D.M., 1982. Power and evolutionary fitness of teleosts. Can. J. Fish. Aquat. Sci. 39, 3–13.

Werner, E.E., Gilliam, J.F., 1984. The ontogenetic niche and species interactions in size-structured populations. Annu. Rev. Ecol. Syst. 15, 393–425.

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

such as scouring and siltation associated with flood events.

The fertilized eggs and alevins in each redd are represented in the model as a cohort from the day of spawning to emergence. Day of emergence depends on the temperature regime between spawning and emergence (e.g. Anderson, 1983). We used a quadratic equation for the development rate (R_{dev}, d^{-1}) from fertilization to 50% emergence as a function of temperature. The fractional development 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). Parameter values (a_{dev}, b_{dev}, c_{dev}) for the quadratic equation were estimated separately for the two species using data from Embody (1934) on the number of days required for 50% of a batch of eggs to hatch into alevins at various constant temperatures. We used the results of Elliott (1984) for brown trout to extrapolate, the data of Embody (1934) for both brown and rainbow trout to number of days required for 50% of a batch of eggs to emerge an age 0 trout.

Emergence of alevins from individual redds in the laboratory experiments of Elliott (1984) occurred over a period of 7–15 days. Differences in day of emergence may be caused by intrinsic differences among eggs and 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 over 10 days centered on the expected day for 50% emergence (Van Winkle et al., 1996), where the day of 50% emergence is determined by accumulating daily values for R_{dev} until the day the cumulative sum of fractional development values = 1.0.

2.4.3. Risks of mortality

Although eggs and alevins in a redd are relatively well protected, several risks of mortality still exist, in addition to superimposition (described Section 2.3). In our model, we represent the risk of mortality caused by (1) dewatering, (2) scouring, (3) temperature, and (4) unspecified causes.

Mortality of eggs and alevins due to desiccation, reduced levels of dissolved oxygen, and exposure to extreme air temperatures can occur as flow and water levels decrease. We assume that a redd is dewatered if the cell in which the redd is located is not wetted ($D \leq D_{dewat}$). Each day that a redd is dewatered, the number of eggs or alevins in the redd is reduced by P_{dewat} times the number of eggs originally spawned in that redd, where P_{dewat} is a parameter with a value between 0.0 and 1.0.

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 and Gard (1972) for rainbow and brook trout, report loss of eggs and alevins during spates and floods. 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 bottom water column velocity ($V_{bott} = 0.67 V_{ave}$, m · s^{-1}; Sullivan, 1986):

$$P_{scour} = \frac{e^{v_{bott}}}{1.0 + e^{v_{bott}}}. \qquad (7)$$

The logistic curve is defined by specifying two points through which the function passes (Van Winkle et al., 1996). Velocity coordinates (V_{bott1}, V_{bott2}) for these two points were varied until we achieved our target of scouring 75–80% of the brown trout redds during an actual winter flood event that resulted in very low abundance of age 0 brown trout in the subsequent summer and fall field samples.

Mortality of eggs and alevins caused by temperature alone appears to be limited to temperature extremes (Embody, 1934; Murray and McPhail, 1988). In the model, we define a daily probability of mortality caused by temperature that is 0.0 within an optimum temperature range and that increases linearly to 1.0 as temperature decreases and increases (Fig. 2) (Wismer and Christie,