PCWA-L-475

Transactions of the American Fisheries Society 129:315–332, 2000

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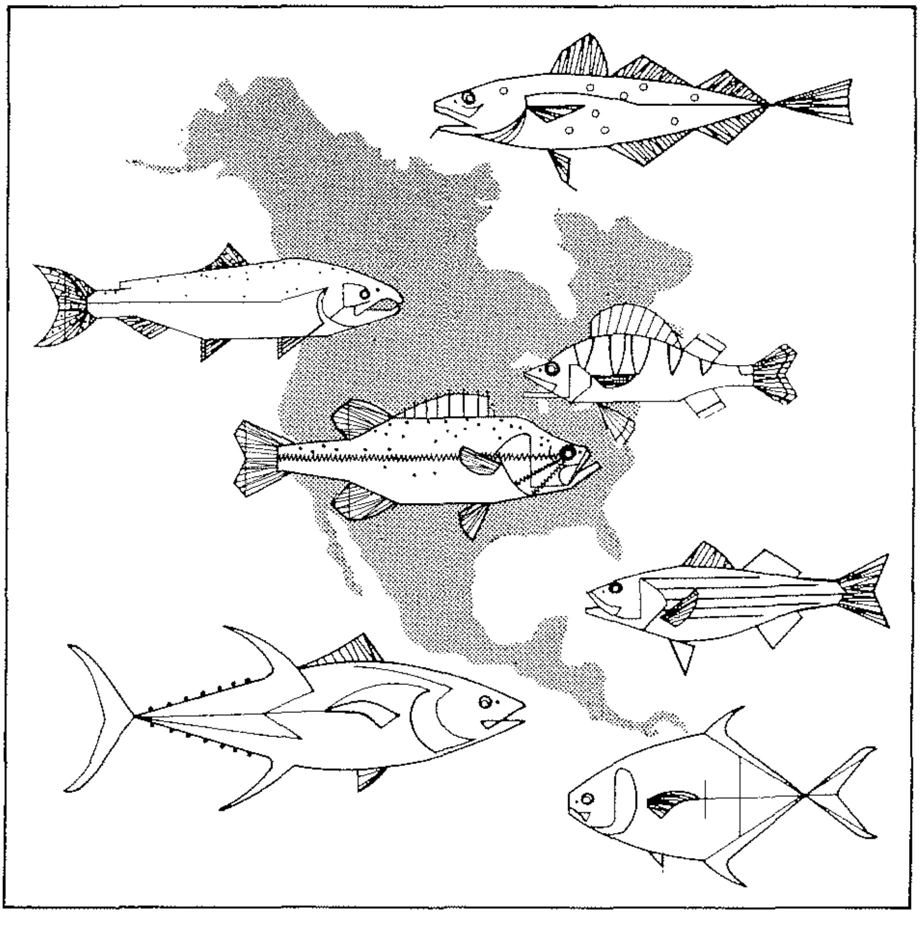
TRANSACTIONS
OF THE AMERICAN FISHERIES SOCIETY

Volume 129 (2) March 2000



AMERICAN FISHERIES SOCIETY

TRANSACTIONS OF THE AMERICAN FISHERIES SOCIETY

VOLUME 129, NUMBER 2, MARCH 2000

(Continued on inside back cover)

ISSN 0002-8487 TAFSAI 129(2) 315–622 (2000)

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OF THE AMERICAN FISHERIES SOCIETY

Volume 129 March 2000 Number 2

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Development and Test of a Whole-Lifetime Foraging and Bioenergetics Growth Model for Drift-Feeding Brown Trout

JOHN W. HAYES,* JOHN D. STARK, AND KAREN A. SHEARER
Cawthron Institute, Private Bag 2, Nelson, New Zealand

Abstract.—We developed and tested a combined foraging and bioenergetics model for predicting growth over the lifetime of drift-feeding brown trout. The foraging component estimates gross energy intake within a fish- and prey size-dependent semicircular foraging area that is perpendicular to the flow, with options for fish feeding across velocity differentials. The bioenergetics component predicts how energy is allocated to growth, reproduction, foraging costs, and basal metabolism. The model can reveal the degree to which growth is limited by the density and size structure of invertebrate drift within the physiological constraints set by water temperature. We tested the model by predicting growth based on water temperature and on drift density and size structure data from postemergence to age 12, and we compared the predictions with observed size at age as determined from otoliths and scales for a New Zealand river brown trout population. The model produced realistically shaped growth curves in relation to the observed data, accurately predicting mean size at age over the lifetime of the trout, assuming 24-h maximum rations and including diurnal drift-foraging costs (predicted versus observed weight $r^2 = 0.94$; length $r^2 = 0.97$). The model predicted that, within a given water-temperature regime, growth is limited primarily by reproduction costs but also by increasing foraging costs as trout grow (a phenomenon that is associated with the increasing foraging time that is required in order to feed to satiation on small invertebrate drift prey). Invertebrate drift size structure significantly influenced predicted growth, especially maximum size, through its effect on foraging time. The model has potential in terms of the exploration of growth-limiting factors and has associated use as an environmental-impact tool and as an aid for hypothesis generation in studies of salmonid growth processes.

Foraging and bioenergetics models are among the most recent tools available for use in evaluating complex biological and biophysical relationships in aquatic ecosystems. These models make a significant contribution to the suite of tools that can be applied to population and growth limiting-factor analysis. For river fisheries, these models offer a way to move beyond some of the limitations of traditional habitat methods of assessing flow needs [e.g., the Instream Flow Incremental Methodology (Bovee 1982; Mathur et al. 1985; Orth 1987)] and of correlative models that relate fish response to environmental and biotic variables (e.g., Binns and Eiserman 1979; Jowett 1992; Nehring and Anderson 1993). Foraging and bioenergetics models are based on functional responses of fish to physical and prey variables, meaning that they can be used to investigate the ultimate causal mechanisms controlling growth and habitat selection. Such models have been used to improve realism in the assessment of salmonid habitat requirements (Smith and Li 1983; Addley 1993; Ludlow and Hardy 1996; Braaten et al. 1997), to predict salmonid distribution at the pool and river level (Hughes 1992a, 1992b, 1998), and to assess salmonid growth and stocking rates in lakes (Kerr 1971; Stewart et al. 1981). Ultimately, energetics-based models have the potential to predict lotic fish carrying capacity as a function of geomorphic, flow, water quality, and food variables.

Foraging models are simplifications of the manner in which fish find and consume their food; these models take into consideration factors such as foraging behavior and swimming speed, prey density and size, and prey capture distance and efficiency (and their dependence on water clarity) (Ware 1972; Vinyard and O'Brien 1976; Fausch 1984; Hughes and Dill 1990; Breck 1993). Bioenergetics models comprise a suite of metabolic equations that quantify functional relationships between water temperature (and other physical variables) and digestion and metabolic, kinetic, and growth processes in fish based on energy as a common unit (Elliott 1976b; Hewett and Johnson 1992; Hayes 1996). Together, foraging and energetics models can be used to determine how fish make a living within a given environment.

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Received July 20, 1998; accepted May 18, 1999

Brown trout *Salmo trutta* have flexible feeding behaviors, but foraging on invertebrate drift predominates in moderate- to swiftly flowing rivers (Bachman 1984; Hayes and Jowett 1994). Invertebrate drift density is a more direct measure of the food that is available to trout than is benthic invertebrate density, or biomass, and it is easier to incorporate invertebrate drift density into a foraging model. Drift-feeding trout maximize net energy intake while minimizing energy expenditure by feeding from sheltered positions into faster water, where drift rates are higher (Fausch 1984), and by selecting large prey from the drift (Ware 1972; Ringler 1979; Wankowski 1981; Bannon and Ringler 1986). Applications of salmonid bioenergetics models in rivers have focused mainly on assessing the relative energetic profitability of drift-feeding sites from estimates of net energy intake (Fausch 1984; Hughes and Dill 1990; Hughes 1992a, 1992b). A logical extension is the accurate estimation of net energy intake and physiological processes to predict growth, estimations that will set the foundation for energetics-based carrying capacity and population dynamics models (cf. Clark and Rose 1997). However, a foundational element in this development is verification that foraging and bioenergetics models can predict actual growth, not simply relative growth and feeding profitability (Addley 1993).

Bachman (1982) proposed a conceptual growth model for drift-feeding salmonids, one that provides a fruitful framework upon which to build a quantitative energetics-based growth model. His conceptual model was based on optimal foraging theory and predicted that growth and size should be limited by the finite energy availability set by the mean drift density for any river. The metabolic rate of salmonids increases exponentially with size, water velocity, and temperature (Elliott 1976b; Brett and Glass 1973), whereas the mean supply of drift increases only linearly with water velocity (Elliott 1967; Fausch 1984). Consequently, growth rate must decline with age, and for a given river, the energy available from drift will limit the maximum fish size, unless the trout migrate to more food-rich habitats or are able to switch to alternative prey with greater energy return. Faced with the increasing energy costs of metabolism and swimming as size increases, and faced as well with reproductive energy costs, trout must eat larger and larger prey as they age in order to maintain growth. If large invertebrates are not well represented in the drift, then large trout should be energetically disadvantaged and their growth truncated.

We are not aware of any published study that has attempted to field test a combined foraging and bioenergetics model for the growth of a drift-feeding salmonid. One study has compared observed with predicted growth of brown trout based on a bioenergetics model, but foraging costs were not accounted for—and neither were reproduction costs—so the comparison was confined to immature fish (Preall and Ringler 1989).

The objectives of this study were (1) to develop and test a combined foraging and bioenergetics model of growth over the lifetime of drift-feeding brown trout at the river section scale, (2) to determine the influence of reproduction and foraging costs on the shape of the growth curve and maximum size within a given river temperature regime, and (3) to determine the influence of invertebrate drift size structure (as it interacts with foraging costs) on growth.

Model Development

Conceptual Framework

Our model is composed of a foraging submodel, a bioenergetics submodel (comprising a suite of energetics equations), and an annual growth submodel. The foraging model uses invertebrate drift density and size composition (3-mm size-classes) and water temperature for a series of user-defined time periods (weeks to months) to calculate rate of food intake and apportion time spent foraging (versus time spent maintaining a position at the focal point or time spent resting). The output from the foraging model and water temperature data are used by the energetics model to calculate daily energy intake, to balance the energy budget, and to calculate growth over each time period. The annual growth model then integrates growth over the time periods for each year, accounting for reproduction costs after maturity.

Geometry of the Foraging Model

The foraging area of a drift-feeding trout can be approximated by delineating a semicircle around the trout, which is positioned close to the bottom of the river at its focal point, which is associated with a velocity refuge—such as a rock (Figure 1). The semicircle should be visualized as a two-dimensional cross section that is perpendicular to the current, looking upstream. The radius of the semicircle, the foraging radius, is represented by *FR*. As drifting invertebrates are carried into this

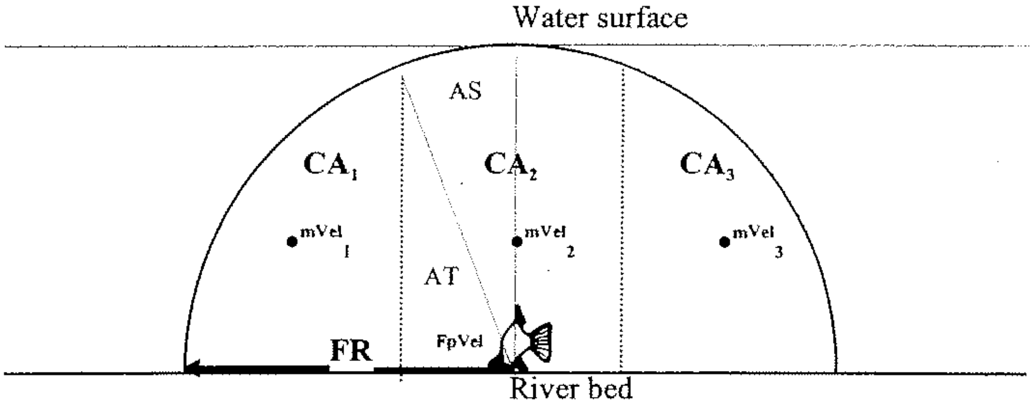

Figure 1.—Cross section of the foraging area (looking upstream), showing how the foraging space is divided to characterize velocities above and adjacent to the trout's focal point. CA_{1-3} = capture areas; AT and AS are subareas used in calculating CA_2 (Table 1); $mVel_{1-3}$ = mean column velocities; $FpVel$ = focal point velocity; and FR = foraging radius.

semicircle by the current, the trout rises upward and/or sideways to intercept the prey and then returns to its focal point. Lateral and vertical velocity differentials (velocity shears) are optional in the model. In order to accommodate for the fact that trout feed across a lateral velocity differential, the semicircle is divided into three strips, with the prey capture areas in each strip represented by CA_{1-3}. The subcapture area CA_2 is calculated by summing the sub-areas (AT and AS), which are formed when the radius (FR) bisects either side of CA_2 into a triangle and a sector of a semicircle (Table 1). The subcapture areas CA_1 and CA_3 can be obtained by halving the remaining foraging area. The mean column water velocities (at 0.4 times depth) of each of the capture areas are represented by $mVel_{1-3}$, and the focal point velocity [at 0.1 times twice the trout's fork length above the substrate (Hayes and Jowett 1994)] is represented by $FpVel$.

We estimated mean velocity of the water column at the trout's position ($mVel_2$) using an equation for the optimal swimming speed of a general salmonid (from Stewart 1980; Table 1). Predictions of this equation matched very well with mean column velocities for adult brown trout in New Zealand rivers (Hayes and Jowett 1994) when temperature was fixed at 13°C, the optimum temperature for growth of brown trout on maximum rations (Elliott 1994).

For the lateral velocity differential option, one of the adjacent mean column velocities assumes the same value as the mean column velocity at the trout's position (in CA_2) (i.e., $mVel_2$), and the other adjacent velocity ($mVel_1$) is calculated by applying a velocity differential to $mVel_2$ over a distance based on two-thirds of the FR (Table 1). For the vertical velocity differential option, the focal point velocity is calculated by applying a velocity differential to the predicted mean column velocity over a distance of twice the fork length of the fish (Table 1).

Foraging radius was calculated as a continuous function of fork length using the conceptual model of the geometry of prey interception, which was developed by Hughes and Dill (1990) for Arctic grayling *Thymallus arcticus* (Table 1). This computation was compatible with modeling growth, in which case predicted size at the end of a given time period becomes the input for calculating consumption and growth in the next time period. Note that the FR increases with both increasing prey size and fish size (because of the greater eye diameter and the retinal acuity of larger fish) and with decreasing water velocity.

Rate of food intake.—The above foraging model was used to calculate rate of food intake, or consumption (C_w), integrated over n 3-mm prey size-classes in the three prey subcapture areas (CA_{1-3}) using a modification of Hughes and Dill's (1990) equation 2 (Table 1). Consumption was calculated for the subset of prey falling within predicted maximum and minimum prey sizes, which are limited by mouth gape, foraging cost–benefit relationships, and gill raker spacing (Wankowski 1979; Bannon and Ringler 1986) (Table 1).

Apportioning foraging time.—Foraging costs, calculated later in the energetics model, were split between total prey-interception time and time spent maintaining station at the focal point. The proportion of time spent intercepting prey items

TABLE 1.—Equations used to estimate the parameters of the drift foraging model.

Parameter or variable[a]	Equation	Source
Subcapture area CA_2 (m^2)[b]	$CA_2 = (AT + AS)$	This paper
CA_2 triangular subarea	$AT = [(\sqrt{FR^2 - (0.33 \cdot FR)^2}) \cdot 0.33 \cdot FR]/2$	This paper
CA_2 semicircle sector subarea	$AS = \}FR^2 \cdot [A \tan\{0.33 \cdot FR/\{\sqrt{FR^2 - (0.33 \cdot FR)^2}\}\}]]/2$	This paper
Subcapture areas $CA_{1,3}$ (m^2)	$CA_1 = CA_3 = \{(\pi \cdot FR^2)/2 - CA_2\}/2$	This paper
Mean column velocity in CA_2 (m/s)[c]	$mVel_2 = 0.097 \cdot W^{0.13} \cdot e^{(0.0405T)}$	Stewart (1980)
Adjacent mean column velocities in $CA_{1,3}$ (m/s)	$mVel_1 = mVel_2 + 0.13 \cdot FR \cdot 0.66$ $mVel_3 = mVel_2$	Based on Hayes and Jowett (1994)
Focal point velocity (m/s)	$FpVel = mVel_2 - (0.4 \cdot 2 \cdot FL - 0.1 \cdot 2 \cdot FL) \cdot 0.6$	Based on Hayes and Jowett (1994]
Reaction distance (m)[d]	$RD_i = [12 \cdot PL_i(1 - e^{(-0.2 \cdot FL)})]/100$	Hughes and Dill (1990)
Foraging radius (m)	$FR = \sqrt{RD^2 - (mVel_2 \cdot RD/V_{max}]^2}$	Hughes and Dill (1990)
Maximum sustainable swimming speed (m/s)[e]	$V_{max} = (36.23 \cdot FL^{0.19})/100$	Jones et al. (1974)
Food intake rate (g dry weight/s)	$C_w = \sum_{i=1}^{n} \left(PC_i \cdot PW_i \cdot \sum_{j=1}^{3} mVel_j \cdot CA_j \right)$	Based on Hughes and Dill (1990): equation 2
Minimum prey length (mm)	$PL_{min} = 0.115 \cdot FL$	Wankowski (1979)
Maximum prey length (mm)[f]	$PL_{max} = 1.05 \cdot FL \cdot 4.3$	Wankowski (1979)
Portion of time spent foraging	$FTsum = \sum_{i=1}^{n} \left(PC_i \cdot (IT + RT) \cdot \sum_{j=1}^{3} mVel_j \cdot CA_j \right)$	This paper
Prey interception time (s)[g]	$IT = 0.5 \cdot RD/V_{max}$	Based on Hughes and Dill (1990)
Return time (s)[g]	$RT = 0.5 \cdot RD/mVel_2$	Based on Hughes and Dill (1990)
Foraging swimming costs (J/h)	$SC = [(a \cdot W^{b_1} \cdot e^{b_2 \cdot T} \cdot e^{b_3 \cdot V})/24] \cdot 4.1868$	Elliot (1976b) and Rand et al. (1993)
Length : weight regression	$FL = e^{\{((\log_e W) + 10.49)/2.842\}}/10$	This paper
Length correction for condition decline with age	$FL_{cor} = (0.0082 \cdot age + 0.955) \cdot FL$	This paper

[a] Definitions:

CA_{1-3} is the subcapture area for trout intercepting drifting prey;
CA_{ij} is the subcapture area for the prey size-class i in subcapture area j;
FL is fork length (cm);
$mVel_j$ is the mean column velocity in subcapture area j;
PC_i is the concentration (number/m^3) of prey size-class i passing within subcapture area j;
PL_i is the length mid-point of prey size-class i (mm);
PW_i is the dry weight (g) of prey size-class i; and
W is fish weight (g)

[b] The area of CA_2 is calculated by summing the triangular and semicircle sector subareas AT and AS (Figure 1).

[c] Water temperature (T) is set to 13°C for calculating $mVel_2$.

[d] Reaction distance (RD) is equivalent to maximum capture distance (MCD) in Hughes and Dill (1990).

[e] The V_{max} equation is that used by Hughes and Dill (1990) for Arctic grayling.

[f] In the equation for PL_{max}, the value 4.3 is an aquatic invertebrate prey length : diameter ratio (personal observation).

[g] Prey interception time (IT) and return time (RT) are based on Hughes and Dill's (1990) equation (1) proof, but a scaling factor of 0.5 is used to approximate mean rather than maximum interception and return time.

and returning to the focal point (FT_{sum}) was integrated over the 3-mm prey size-classes in the three subcapture areas (Table 1). Trout were assumed to be swimming at their maximum swimming speed (V_{max}) when intercepting prey and at their optimal swimming speed ($mVel_2$) when returning to their focal points. The proportion of the foraging time spent at the focal point is $1 - FT_{sum}$. When drift rate exceeds the time taken for a trout to intercept a prey item and return to the focal point, the trout is assumed to remain up in the water column in a constant prey-interception maneuver mode, at which time the trout is experiencing V_{max} swimming costs. This situation models peak feeding behavior such as the kind that occurs during insect hatches, although V_{max} may overestimate swimming speed for this foraging mode.

Bioenergetics Model

The bioenergetics model was based on the following energy balance equation (Elliott 1994),

TABLE 2.—Equations used to estimate the parameters of the energetics model. Parameter values for the various equations are given in the Appendix.

Parameter	Equation	Source
Maximum energy intake (consumption) (J/24 h)	$C_{\max} = a \cdot W^{b_1} \cdot e^{b_2 T} \cdot 4.1868$	Elliot (1976b)
Energy losses in faeces (J/24 h)	$F = C_e \cdot (a \cdot T^{b_1} \cdot e^{b_2 \cdot (C_e/C_{\max})}) \cdot 4.1868$	Elliot (1976b)
Energy losses in urine (J/24 h)	$U = C_e \cdot (a \cdot T^{b_1} \cdot e^{b_2 \cdot (C_e/C_{\max})}) \cdot 4.1868$	Elliot (1976b)
Standard and maximum metabolism (J/24 h)	$R_s, R_{\max} = a \cdot W^{b_1} e^{b_2 T} \cdot 4.1868$	Elliot (1976b)
Metabolic cost of digestion (J/24 h)	$R_d = (R_{\max} - R_s) \cdot 4.1868$	Elliot (1976b)
Maximum meal size (g)	$Q = a \cdot W^{b1} \cdot e^{b_2 T}$	Elliot (1975c)
Meal interval (h)[a]	$I = \begin{cases} a \cdot e^{-bT} & \text{if } I \geq \text{satiation time} \\ \text{satiation time} & \text{if } I < \text{satiation time} \end{cases}$	Elliot (1975b) and this paper
Number of meals[b]	$N_m = h/I$	Elliot (1975b)
Gastric evacuation rate[c]	$LnY_X = 4.6052 - X \cdot 0.053 \cdot e^{0.112 \cdot T}$	Elliot (1972)
Trout energy density[d] (J/g)	$ED = \begin{cases} 3{,}148 \cdot e^{0.332 \cdot K} \cdot W^{0.072} & \text{if } W \leq 810 \text{ g} \\ 7{,}452 & \text{if } W > 810 \text{ g} \end{cases}$	Elliot (1976a) and Lien (1978)

[a] Meal interval is the period from the start of one meal to the start of the following meal.

[b] In the equation, h is hours which can be set to 24 h or to hours of daylight.

[c] Percent of meal remaining at time X (h).

[d] In the equation, K (condition factor) = $100 \cdot W/FL^3$.

which was solved on a daily time step for the average individual:

$$\Delta B = C_e - F - U - (R_a + R_s + R_d). \qquad (1)$$

In this equation, ΔB is the energy accumulated for growth and reproduction, C_e is consumption (expressed as daily energy intake), F and U are the energy losses in feces and urine, R_a and R_s are the energy requirements for active and standard metabolism, and R_d is the energy required for digestion (including specific dynamic action).

The primary source for equations for the components of the energy budget (other than C_e) was the series of studies that Elliott conducted on the energetics of brown trout (summarized in Elliott 1976b, 1994) (Table 2). Elliott's energetics equations were developed on 5–300-g brown trout in tanks. These equations were extrapolated to larger trout (2,500 g or more) in our bioenergetics modeling. Extrapolation of bioenergetics equations outside the size ranges of the fish upon which the equations are developed can introduce errors but is common in bioenergetics modeling because equations for large fish are rare (Ney 1993). Components of the bioenergetics equation that are not obtainable from Elliott's papers were obtained from other sources, including studies on rainbow trout *Oncorhynchus mykiss* and salmonids in general (Stewart 1980; Rand et al. 1993) (Tables 1, 2).

We approximated R_d by subtracting R_s from $R_{\max}$ (metabolism at maximum rations) (Table 2). Elliott was not able to isolate R_d from R_a, but he considered R_a to be a minor component of the metabolic rate in his experiments (Elliott 1976b, p. 944). We therefore assumed that $R_d + R_a$ in Elliott (1976b) approximated R_d.

Daily energy intake.—Consumption (C_w in grams per second) (Table 1) was used to estimate daily energy intake. Satiation time for diurnal drift feeding and meal size were determined from the food intake and gastric evacuation rates (Table 2). Gastric evacuation rate, maximum meal size, the interval between meals, and the number of meals per diurnal and 24-h foraging periods were determined from equations in Elliott (1972, 1975b, 1975c) (Table 2). Following a meal, trout were assumed to remain satiated (i.e., not commencing with feeding) until 80–90% of the meal was evacuated (cf. Elliott 1975b). Daily consumption was calculated as the product of the size and number of meals per day converted to energy intake (J/d) using the average prey energy value.

Foraging costs.—Total satiation time (summed for all meals) was split by FT_{sum} and $1 - FT_{\text{sum}}$. Swimming costs (*SC*) for each of these activities were calculated by combining standard metabolism for brown trout (from Elliott 1976b) and velocity-dependent active metabolism for rainbow trout (Stewart 1980 [from Rao 1968]; Rand et al. 1993) (Table 1). Active metabolism could be op-

TABLE 3.—Physical data from the Maruia River for the eight time periods used to model trout growth (hours of daylight are defined by light intensity >0.02 lx).

Time period	Time period (number of days)	Hours of daylight	Water temperature (°C)
1 Oct–9 Nov[a]	40	15.0	10.3
10 Nov–7 Dec	28	16.8	13.4
8 Dec–31 Dec	24	17.0	14.9
1 Jan–29 Jan	29	16.8	16.5
30 Jan–7 Mar	37	15.8	16.9
8 Mar–20 Apr	44	12.9	13.0
21 Apr–28 Jul	99	11.8	7.8
29 Jul–30 Sep[a]	64	12.7	7.0

[a] The first and last time periods use data from the same drift sampling occasion.

tionally set to zero in the model when trout were assumed to be resting. Note that activity cost estimated by SC is additional to the latent activity cost, R_a in the R_d estimated from Elliott (1976b). Elliott's experimental fish were maintained in flow-through tanks with minimal mean velocity (based on tank dimensions and flow given in Elliott 1975a). Drift-feeding trout in the wild are faced with added activity costs associated with swimming at their focal point and foraging into the faster surrounding water. The foraging cost calculated in our model may therefore be slightly overestimated (by the unavoidable inclusion of R_a), but this overestimation may be somewhat offset by unknown activity costs during satiation periods, costs that were assumed to be zero in most of our growth-modeling scenarios.

Annual Growth Model

The change in energy (ΔB) over each time period estimated by the energetics model was converted to weight using an estimate of energy density for brown trout, one that was dependent on fish size and condition (Elliott 1976a; Lien 1978) (Table 2).

Reproduction costs were obtained from Lien (1978), who studied the energy budget of a Norwegian lake population of brown trout. Lien found that the energy content of mature trout was reduced by an average of 46% (males 44%, females 48%) after spawning, including losses in gonads and body tissue. Body weight was reduced by only 18%; the difference between the body weight reduction and energy content made up by water balance.

Upon reaching a user-defined mature weight, the model reduces the trout's energy content by 46% and its weight by 18% at the end of the current growth season. These reductions place the trout in energy deficit for the next growth season. The energy deficit must first be met before energy is available for growth. Annual growth is integrated over the subannual time periods, and the modeling is repeated for 12 years.

Model Testing

The data used for testing the model were collected from the Maruia River in South Island, New Zealand (lat. 42°06′, long. 172°12′; altitude, 300 m). The river has a gradient of 0.003 over the study section and mean, median, and mean annual 7-d low flows of 60, 40, and 24 m^3/s, respectively. We chose a study section above the Maruia Falls, which isolated the brown trout population upstream and guaranteed that we were dealing with resident fish. Brown trout are the predominant salmonid present in the river; rainbow trout are also present, but they are rare. The trout are large (most angler-caught fish are 40–65 cm), and abundance and biomass are relatively low (approximately 30 kg/ha; Nelson-Marlborough Fish and Game Council, unpublished drift dive data) (cf. Behnke 1992) but typical of New Zealand inland and high-country, freestone rivers.

Physical Variables and Drift Sampling

Water temperature was logged continuously at 15-min intervals in the Maruia River for 1 year (1994–1995) and was then condensed to daily means and then to a single mean for a series of time periods centered on the dates of invertebrate drift sampling (Table 3).

Invertebrate drift was measured on seven occasions over the 1-year period (1994–1995). On each occasion, drift was sampled for a 24-h period at three sites along a 0.8-km reach of river. At each site, three 0.0052 m^2 (0.5-mm mesh) drift samplers (modified from Field-Dodgson 1985) were stacked vertically in the water column at 0.1 m, 0.4 times depth, and at the surface. Water velocity was re-

TABLE 4.—Invertebrate drift densities (number per m^{-3}) from Maruia River for the eight time periods used to model trout growth.

Time period start date	Invertebrate size-class midpoints (mm)										
	1.5	4.5	7.5	10.5	13.5	16.5	19.5	22.5	25.5	28.5	37.0
1 Oct[a]	1.221	0.584	0.189	0.110	0.030	0.019	0.006	0.004	0.001	0	0
10 Nov	0.575	1.087	0.407	0.114	0.040	0.011	0.004	0.001	0	0	0
8 Dec	2.031	1.349	0.333	0.085	0.013	0.007	0.003	0.001	0.001	0.001	0
1 Jan	2.835	1.425	0.333	0.079	0.019	0.005	0.001	0	0	0	0.001
30 Jan	2.354	2.048	0.660	0.109	0.020	0.009	0	0	0	0	0
8 Mar	3.250	0.534	0.585	0.137	0.025	0.012	0.005	0	0	0	0
21 Apr	2.206	0.466	0.174	0.046	0.027	0.017	0.009	0.002	0.003	0.002	0
29 Jul[a]	1.221	0.584	0.189	0.110	0.030	0.019	0.006	0.004	0.001	0	0

[a] The first and last time periods use data from the same drift sampling occasion.

corded with a Pygmy current meter at the mouth of each sampler after installation and prior to changing of nets in order to determine the volume sampled. Mean drift density (number of invertebrates/m^3) was determined within each site and between sites.

The 24-h drift samples were split into day and night periods, and only the day samples were used in testing the bioenergetics model. The day period (foraging hours; Table 3) was defined by a period of light intensity of greater than 0.02 lx, which was assumed to approximate the 50% reaction distance threshold for brown trout feeding on drifting prey (Robinson and Tash 1979). Light intensity at dawn and dusk was measured with a Gossen Panlux light meter that was accurate to within 0.5 lx and that was extrapolated graphically to 0.02 lx.

In the laboratory, invertebrates were sorted into 3-mm size-classes and identified to the species or genus level for common taxa and to the family or order level for rare taxa. Dry weight and energy value (joules) for each taxon and size-class were determined from length : dry weight and dry weight : energy relationships from the literature (Cummins and Wuycheck 1971; Sage 1982; McCarter 1986; Sample et al. 1993; Towers et al. 1994) and from our own unpublished data, and values were condensed to weighted averages for bioenergetics modeling.

Drift density data collected from the Maruia River are presented in Table 4. The smallest size-classes had the highest drift densities; invertebrates of less than 15 mm comprised 94% of the annual drift biomass, with 74% of the biomass in the 6–12-mm range. Drift was sampled on seven occasions, but data for eight time periods are presented in Table 4 because we split one of the drift sampling periods that straddled the trout's birth date (1 October).

Trout Samples

Growth data were obtained from a sample of 37 brown trout (>20 cm in length) caught (by angling) in a 25-km section of the Maruia River (surrounding our drift sampling sites) over the course of the 1994–1995 summer. Samples of smaller trout (27 fish) were taken by electrofishing the lower reaches of two tributaries that entered our study section. Trout were aged from thin transverse-sectioned sagittal otoliths, and scales were also used to verify the ages of 1- and 2-year-old fish. Age and size at first spawning were estimated from visual examination of gonad development of angler-caught fish.

Length : Weight Conversion

Length : weight conversions made in the bioenergetics model were based on a functional regression that was calculated for the 64 Maruia River brown trout ($r^2 = 0.99$) (Table 1). The model output was weight at age. Length at age was calculated from predicted weight using the length–weight relationship, with a correction applied to account for a significant decline in condition with age ($F = 26.4$, df = 63, $P < 0.001$) (Table 1).

Model Settings

For each modeling run, the initial weight of trout was 1 g, the weight threshold for spawning (for reproduction costs) was set at 1,500 g, and growth was modeled for 12 years. We used 1 October as the birth date for trout in the Maruia River; this age was determined from knowledge of emergence patterns and from approximate time of annulus formation in otoliths.

Both vertical and lateral velocity differentials were chosen for the foraging model. Water clarity was assumed not to limit prey reaction distance. Modeling scenarios were undertaken to systematically examine the sensitivity of model predictions to food intake relative to maximum ration, reproduction, foraging activity, and continuous activity. As no a priori information was available on activity budget, the foraging activity scenario assumed that trout rest when satiated. The continuous activity scenario involved fish continuously experiencing focal point velocity swimming costs, except when they were intercepting prey, at which time they experience V_{max} and $mVel_2$ swimming costs.

Modeling Growth on Variable Invertebrate Drift Size Structure

In order to explore the sensitivity of predicted growth to invertebrate drift size structure, we ran the model using Maruia drift, with modifications made to its size structure. Two modified drift size structure scenarios were modeled: (1) invertebrates larger than 9 and (2) invertebrates larger than 12mm were omitted from the input data, and drift densities of invertebrates that were less than 6 mm were increased to keep total prey biomass constant. Energy density was standardized to 20,934 J/g dry weight for all drift prey size-classes. For these experiments, the minimum prey size condition used in the foraging model, 0.115 × *FL*, (Wankowski 1979), was removed (i.e., minimum prey size was set to zero) to ensure that differences in predicted growth were entirely the result of foraging energetics and not simply a result of a difference in the proportion of available prey overlooked by larger fish.

Determining Model Fit

Model fit was assessed by regressing observed on predicted growth and by using the method of partitioning the mean squared error (MSE), which was summarized by Rice and Cochran (1984). The procedure serves as a diagnostic check of the degree and sources of error in model predictions. The mean squared error is partitioned as follows:

$$MSE = \frac{1}{N}\sum_{i=1}^{n}(E_i - O_i)^2$$
$$= (\bar{E} - O)^2 + (S_E - r \cdot S_O)^2$$
$$+ (1 + r^2) \cdot S_O^2 \qquad (2)$$

In this equation, E_i and O_i are the predicted (expected) and observed series, $\bar{E}$ and $\bar{O}$; S_E and S_O are the means and standard deviations of the series E_i and O_i; and r is their correlation coefficient.

Following Rice and Cochran's description, partitioning of *MSE* can be interpreted in relation to a least-squares regression of observed values (O_i) on predicted values (E_i). In the ideal case, all points would fall on the 1:1 line, and the regression would have a slope of one and an intercept of zero. *MSE* represents the variance of these points around the 1:1 line. Dividing the components of the partitioned *MSE* above by the *MSE* yields the proportions of the *MSE* that were attributed to three different sources of error: *MC* equals the mean component (the bias attributable to the differences in the means of predicted and observed values), *SC* equals the slope component (the error resulting from the slope's deviation from unity), and *RC* equals the residual component (the proportion of the *MSE* that is attributable to random error). When perfect predictions ($MSE = 0$) cannot be obtained, the desirable distribution of *MSE* over the three sources of error is $MC = 0$, $SC = 0$, and $RC = 1$; this distribution indicates that errors are not systematic. The significance of systematic errors represented by *MC* and *SC* can be tested against the joint null hypothesis that the regression of O_i on E_i has a slope of one and an intercept of zero.

Results

Predicted Versus Observed Growth

Initial modeling trials based on the Maruia physical and drift data indicated that food intake rate was sufficient for trout to achieve satiation relatively quickly and therefore to allow them to obtain maximum rations (i.e., to meet C_{max}; Table 2). For example, diurnal drift-feeding satiation times at the warmest summer water temperatures (14.9–16.9°C) ranged between 2.8 and 100 min for 40 and 2,000 g trout, respectively, whereas the expected minimum interval between meals was 8.4 to 10.6 h (Elliott 1975b). This rapid satiation justified using R_{max} to estimate R_d in the bioenergetics model.

Predicted growth, assuming that trout fed only during the hours of daylight and including reproduction and diurnal foraging costs, substantially underestimated observed growth (Figure 2A). Predicted diurnal consumption occurred at a maximum rate for the temperatures modeled, but sum diurnal consumption fell short of theoretical 24-h maximum consumption (Elliott 1975b, 1976b). The explanation for this limitation is that, based on the temperature and light data recorded for the Maruia River, there were insufficient hours of daylight for fish to consume and process enough meals per day to achieve maximum daily energy intake

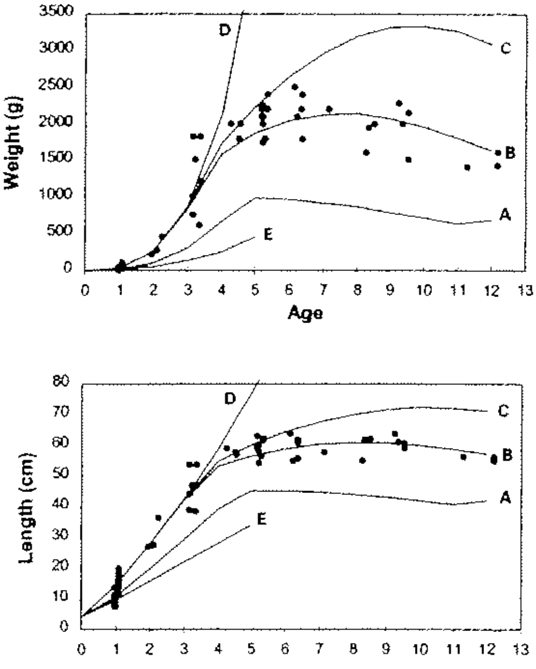

Figure 2.—Comparison of predicted and observed (filled circles) weight and length at age of brown trout for the Maruia River under five growth-modeling scenarios. Scenario A assumes that trout feed only during the hours of daylight and includes diurnal drift-foraging and reproduction costs. Scenarios **B–E** assume that trout achieve maximum 24-h energy intake by feeding day and night. Scenario **B** includes diurnal drift-foraging and reproduction costs, C includes only reproduction costs, **D** has no drift-foraging or reproduction costs, and **E** includes diurnal drift-foraging and reproduction costs and continuous focal point swimming costs.

(C_{max}) and to thereby grow at their maximum rate. For example, the model predicted a maximum of two meals consumed during daylight hours for the warmest summer water temperatures (14.9–16.9°C), with the last meal potentially digested during the night, compared with the expected maximum number of meals, 2.26–2.86, over a 24-h period (Elliott 1975b). In other words, in order to fit the observed growth of trout in the Maruia River, it must be assumed that the trout obtained part of their daily food intake by feeding at night.

Unfortunately, we were unable to simulate nocturnal foraging behavior and associated prey capture costs. To approximate a 24-h feeding regime, we forced the model to maximum 24-h rations and applied diurnal drift-feeding foraging costs. Total foraging costs may have been only slightly underestimated with this approach, because diurnal drift feeding could account for 87–89% of annual maximum energy consumption (i.e., annual C_{max}). This modeling scenario produced realistically shaped growth curves in relation to the observed growth data, with a good fit to mean size at age over the lifetime of the trout (Figure 2B) (the regressions of predicted versus observed weight and length had r^2 values of 0.94 and 0.97, respectively). Predicted onset of reproduction occurred at age 3–4, 1 year earlier than for the diurnal modeling scenario above (i.e., Figure 2A). Partitioned *MSE* for predicted weight indicated that almost all of the variance was attributable to random variation rather than to systematic errors ($MC = 0.02$, $SC = 0.02$, $RC = 0.96$), and the 95% confidence region for the slope and intercept of the regression of observed on predicted weight included a slope of one and an intercept of zero. Predicted length included moderate systematic error in the slope component, but again, most of the variation was attributable to random error ($MC = 0.02$, $SC = 0.19$, $RC = 0.79$). The 95% joint confidence region for the slope and intercept of the regression of observed length on predicted length did not include a slope of one nor an intercept of zero. The error in the slope component was attributable to an overestimation by the model of length at age 1 (predicted length, 15.4 cm; observed mean length, 12.5 cm). Predicted weight at age 1 (53.5 g) also overestimated observed mean weight (35.5 g), but the greater variation in observed weight than in observed length, especially at older ages, dominated the *MSE* for weight. In other words, the 95% confidence regions around the regression of observed versus predicted weight were wider than those for length.

The influence of drift-feeding foraging costs on growth in the above modeling scenario can be seen by comparing growth curves B and C in Figure 2. The latter is predicted growth on maximum rations, including reproduction costs but not foraging costs. Foraging costs increase with fish size and compound with growth to have a very substantial influence on maximum size. The influence of reproduction costs on growth can be seen by comparing growth curves C and D in Figure 2. The latter is growth on 24-h maximum rations in the absence of reproduction and foraging costs.

The combined effects of reproduction and increasing foraging activity costs flatten the predicted growth curve and eventually cause weight to decline. Predicted weight declines at older ages because progressively more time is required for fish to recover the energy deficit incurred from the

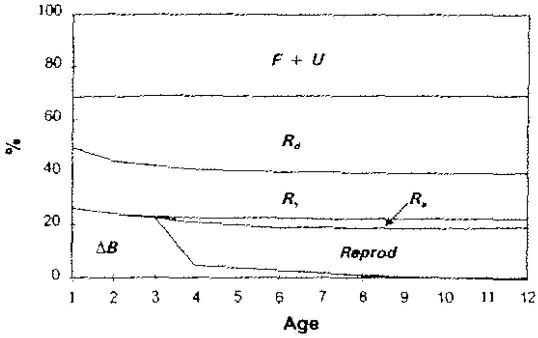

Figure 3.—Predicted percent annual energy consumption spent on the various components of the energy budget for growth-modeling scenario **B** (see Figure 2). F and U denote energy lost in feces and urine; R_d, R_s, and R_a denote metabolic energy costs of digestion, standard metabolism, and activity; and ΔB and *Reprod* denote energy invested in growth and reproduction.

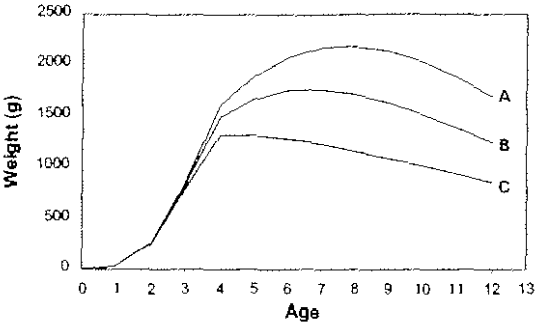

Figure 4.—The influence of invertebrate drift size structure on trout growth using the growth-modeling scenario **B** (see Figure 2). Predicted growth curves are based on the unmodified drift data from the Maruia River (**A**) and Maruia River drift data with invertebrates larger than 12 mm (**B**) and 9 mm (**C**) omitted and with the density of invertebrates of less than 6 mm increased to keep total biomass the same as in **A**.

previous season's spawning. Foraging costs increase with fish size (and age) because limited drift prey size requires an increase in the proportion of time spent foraging in order to meet daily energy requirements or to achieve satiation. For example, based on the modeling results for the Maruia River physical and drift data in midsummer (water temperature, 16.9°C), a 120-g (22-cm) trout would require 8 min foraging time to satiate per meal, whereas a 2,135-g (60-cm) trout would require 90 min foraging time to satiate.

The relative predicted annual cost of foraging activity was small by comparison with the energy allocated to reproduction (Figure 3). For the modeling scenario that best fitted the observed growth data (Figure 2B), foraging activity costs accounted for 0.03 (age 1) to 3.7% (age 8) of annual energy consumption, depending on the age and size of the fish, whereas reproduction accounted for 16 (age 4) to 20% (age 12) (Figure 3).

The energy costs of activity and of reproduction appear to be much more significant when viewed as the percentage of the total energy available for growth, reproduction, and activity (i.e., the energy surplus to that lost in body wastes and used for digestion and standard metabolism). Viewed in this manner, foraging activity and reproduction costs represented 0.1 (age 1) to 16.6% (age 8) and 72 (age 4) to 89% (age 12), respectively, of the energy surplus to basic body requirements.

The influence of continuous swimming costs on growth potential are demonstrated by growth curve E in Figure 2. This growth prediction is based on 24-h maximum rations, reproduction, and foraging costs, but it includes continuous drift-feeding focal point swimming costs. Predicted growth was very much lower than it was in the scenario that assumed that trout rest when satiated (Figure 2B). The slow growth also means that mature weight (1,500 g) cannot be attained until age 8, and thereafter, reproduction occurs only every second year. This resulted in an unrealistic growth curve over the lifetime of the trout, so predicted size at age for this scenario was presented for comparative purposes only for 5 years.

The Influence of Invertebrate Drift Size Structure on Growth

The modeling scenarios with modified invertebrate drift size structure demonstrate that limited prey size in the drift can potentially significantly limit trout growth (Figure 4). Predicted growth for the modified drift size structures was depressed substantially after age 3 compared with that predicted for the unmodified Maruia drift data; maximum predicted weight declined by 19 and 44%, respectively, when maximum prey size was reduced from 39 to 12 and 9 mm, respectively (Figure 4). The reduction in growth potential was the result of the increased foraging time required for satiation as prey size declined rather than the result of "food limitation," because maximum daily energy intake was maintained throughout these modeling scenarios.

Discussion

Modeling Assumptions

Our drift-feeding bioenergetics model produced realistically shaped growth curves in relation to the observed growth data, accurately predicting mean size at age over the lifetime of the trout, assuming maximum 24-h energy intake and including reproduction and diurnal drift-foraging costs (Figure 2B). The assumption of maximum 24-h energy intake required that trout fed during the night as well as during the day. We were not able to estimate nocturnal foraging costs but considered that the error incurred in our growth estimation as a consequence of omitting these may be relatively small. In support of this view, predicted diurnal drift prey consumption could account for 87–89% of annual maximum food intake (minimum in winter of 71%, maximum in spring and early summer of 100%).

The field evidence for whether river trout predominantly feed during the day or at night, regardless of prey type, is equivocal. Diurnal feeding by stream salmonids has been reported in several studies (Sagar and Glova 1987; Glova and Sagar 1991; Young et al. 1997a), but others have reported nocturnal feeding or both diurnal and nocturnal feeding (Chaston 1969; Jenkins 1969a; Elliott 1970; Feldmeth and Jenkins 1973; Clapp and Clark 1990; Young et al. 1997b). Perhaps the strongest evidence for the necessity of nocturnal (in addition to diurnal) feeding is Elliott's (1975b) estimate of the number of meals per day and of the interval between meals for brown trout growing on maximum rations in experimental tanks. Daily energy intake and number of meals per day increase with water temperature (Elliott 1972, 1975c, 1976b). When temperature exceeds 13°C (as it did for most of the summer in the Mariua River), trout must feed at night as well as during the day if they are to achieve maximum 24-h energy intake and to realize maximum growth potential. Whether or not maximum 24-h consumption can be theoretically achieved by diurnal foraging alone depends on the balance between water temperature and hours of daylight. The above fact raises the interesting corollary that if trout are able to obtain sufficient food at night at higher temperatures, then they presumably can do likewise at lower temperatures. If so, then in cold water trout, especially small individuals and juveniles, could conceivably obtain all of their daily food requirements at night and could rest in cover during the day to minimize predation risk. This view is consistent with observations of nocturnal activity and feeding and daytime substrate hiding reported for trout in north temperate winters (Heggenes et al. 1993) and in coolwater conditions in New Zealand (Hayes and Baird 1994). However, if the above view is correct, then it highlights a shortcoming of focusing foraging models on diurnal drift-foraging behavior, as we did.

The current version of our bioenergetics model is not able to estimate nocturnal foraging costs. Such an estimate could potentially be achieved by including a light-intensity function in the estimation of prey reaction distance. The profitability of drift feeding may become marginal at night, because the reaction distance to small prey has an asymptotic relationship with light intensity—rapidly declining at low light levels (Vinyard and O'Brien 1976; Robinson and Tash 1979; Henderson and Northcote 1985; Hughes and Dill 1990)—but this limitation may be offset by the higher drift densities and general activity of aquatic invertebrates at night (McLay 1968; Elliott 1970; Waters 1972; Brittain and Eikeland 1988). These uncertainties highlight the need for research to assess the relative importance of drift feeding versus alternative foraging strategies for trout feeding at night (and also during the day).

The good fit of our model predictions to the observed size-at-age data supports the assumption that trout rest when satiated. Intuitively, it makes sense that fish should rest when they are not feeding, unless they are involved in behavioral interactions, predator avoidance, or migration, but the documented evidence for this possibility is equivocal. Some studies support the above contention, showing that stream salmonids seek low-velocity (resting) areas at night or when drift density is low (or between bouts of drift feeding) (Edmundson et al. 1968; Jenkins 1969b; Fausch 1984; Hughes 1991; Campbell and Neuner 1995). However, others have reported that trout hold drift-feeding positions continuously throughout the day (Bachman 1984) and also at night (Jenkins 1969a). The latter observations can be reconciled with our modeling predictions if trout select very low focal point velocities to allow prolonged foraging when drift densities are low (cf. Bachman 1984).

The simple assumption of constant reproduction costs takes no account of potential trade-offs between growth and reproductive investment versus age and differences between populations (Wooton 1985). Moreover, the reproduction costs that we applied were based on only one study of brown trout in the northern hemisphere (Lien 1978). Given this limitation, it is somewhat surprising that our model fit the observed size-at-age data so well (Figure 2B). Unfortunately, studies estimating complete reproductive losses in salmonids are rare. It is tempting to interpret the decline in observed size with age (>10 years) exhibited by the Maruia River trout as evidence that corroborates the constant reproductive-cost assumption. However, this pattern of observed growth might simply be attributable to size-selective mortality that operates on the faster growing individuals in a population, with the slower growing fish surviving to a greater age (Ricker 1979).

Factors Influencing Predicted Growth

We did not undertake an exhaustive sensitivity analysis. Instead we concentrated on the influence of key physiological and foraging variables that we considered most important in determining the shape of the growth curves and in setting maximum size. Moreover, our sensitivity analysis was carried out within a single river temperature regime. Over a broader geographic scale, the factors discussed below will operate within the overriding influence of water temperature on growth (Elliott 1994).

Putting temperature aside, the bioenergetics modeling scenarios that formed the basis of our sensitivity analysis provide some general insights into growth processes in stream salmonids. When unconstrained by reproduction costs and ration, theoretically growth would continue to increase exponentially (cf. Figure 2D). The departure from exponential growth after age 3 in our growth predictions for the Maruia River (Figure 2B) is the result of the combined effects of reproduction costs and increased foraging costs related to increased foraging time. Together, reproduction and foraging costs set an upper limit to predicted trout size. This boundary is consistent with the conceptual model postulated by Bachman (1982, 1984), which holds that growth and asymptotic size should be limited by the finite energy of the drift in relation to the energy demands of capturing food, producing gametes, and reproductive behavior.

Constant reproduction cost in the bioenergetics model drives the pattern of decline in predicted weight and, to a lesser extent, the length of older trout (Figure 2B, C). Constant reproduction cost coupled with the increasing foraging cost faced by large trout place the fish in an increasing energy deficit spiral, which eventually results in the mining of body weight to support reproduction. Age at maturity can also affect the growth trajectory, but it has little effect on predicted maximum size.

The model predicted that small trout had minimal foraging cost because they could satiate very quickly on the high drift densities recorded from the Maruia River. This projection is partly a result of the assumption in our prey capture algorithm that trout select first the largest prey within the range of potential prey size classes (Table 1). This bias in the prey capture algorithm may have caused the relatively small overestimation of size at age 1, which contributed to the moderate systematic error in the slope of the growth in length curve. A random prey size selection algorithm, or one weighted to the optimal prey size, may be more appropriate.

Nevertheless, the prediction that small trout have minimal foraging costs and short satiation times still holds for the Maruia River, because drift rates are high, and the mean size of invertebrates is comparatively large in relation to the size of small trout. Therefore, the inference from our modeling is that food-processing time is the major growth-limiting factor for immature trout in this river (cf. Crow 1981).

High drift densities and short satiation times for small trout mean that growth predictions made in our test of the bioenergetics model in the Maruia River were relatively insensitive to error in the foraging model, especially for small fish. Shortcomings in foraging models are more likely to be apparent in rivers with low drift densities, in which foraging costs will be more significant and will be exacerbated by high water temperatures.

Our modeling scenarios predict that foraging energetics become more limiting as trout grow, because longer foraging times are required to satiate on drifting invertebrate prey, and this situation is exacerbated by high water temperature. Preall and Ringler (1989) found evidence for a decline in the growth potential of brown trout between age-1 and -2 trout and suggested that increased drift-foraging costs might be responsible. Addley (1993) also predicted an increase in satiation time with size based on the results of foraging and bioenergetics modeling on drift-feeding cutthroat trout in an Idaho stream, but he reported longer satiation times than we did, because drift densities and invertebrate size were much lower in his study stream than in the Maruia River. Prey size selection by stream salmonids is well known (Ware 1972; Ringler 1979; Wankowski 1981; Dunbrack and Dill 1983), and some authors have suggested that production of large trout depends on the availability of large invertebrates (Bannon and Ringler 1986; Clapp and Clark 1990; Fausch 1991; Messick 1995). Kerr (1971) accurately predicted the growth of piscivorous lake trout with a bioenergetics model and demonstrated that decreased foraging efficiency on small prey reduced predator size.

The above discussion sheds new light on the concept of food limitation in stream salmonids. Our modeling results demonstrate that it is possible for growth to be "limited" while the fish are obtaining maximum rations. In fact, growth will be limited by increasing foraging costs with fish size long before drift-feeding salmonids fail to obtain their maximum daily food intake. This restriction suggests that studies aimed at assessing food limitation by examining gut fullness have limited value, especially for small trout.

The modeling scenario with continuous swimming costs clearly showed that trout cannot afford to spend all of their time swimming at their drift-feeding focal points, at least not at the focal point velocities recorded for New Zealand drift-feeding brown trout (Shirvell and Dungey 1983; Hayes and Jowett 1994). Our model predictions provide theoretical evidence for the need for trout to minimize activity when they are not feeding in order to maximize their growth potential. Habitat structure is usually considered important for stream salmonids (from the point of view of providing low-energy drift-feeding locations) (Bachman 1984; Fausch 1984; Hayes and Jowett 1994; Braaten et al. 1997). The strong influence that time spent resting has on growth, as demonstrated by our model predictions, also highlights the potential energetic importance of resting habitat.

Large Brown Trout in New Zealand Rivers

The Maruia River brown trout, which are typical of drift-feeding trout in New Zealand inland and high-country rivers, appear to be large in comparison with North American river-resident trout (cf. Bachman 1984; Bannon and Ringler 1986). The paradigm for north temperate rivers—that trout must switch at a relatively small size (20–30 cm) from a diet of invertebrates to one of fish or crayfish or that they must migrate to more food-rich habitats in order to continue to grow (Allen 1969; Bachman 1984, 1991; Bannon and Ringler 1986)—does not appear to hold for many New Zealand rivers. Typically, New Zealand high-country and inland rivers support comparatively low densities of large trout (up to 60 cm or more) predominantly on invertebrate drift. Although temperature differences cannot be discounted as an underlying cause of the apparent difference in growth potential between north temperate and New Zealand rivers, it is an interesting speculation that New Zealand rivers, especially in their headwaters, may have unusually high diurnal drift densities of large invertebrates.

It is unclear whether population density needs to be considered when applying our bioenergetics model. High population density generally has been considered to retard trout growth (Backiel and Le Cren 1978), but more recently this view has been questioned for stream salmonids (Bachman 1984; Preall and Ringler 1989; Elliott 1994). The low density of trout coupled with high drift densities, predicted maximum daily energy intake, and the fact that observed growth tracked theoretical growth rate on maximum rations, suggests that growth is not density dependent in the Maruia River. Nevertheless, when trout density is high enough, dominant fish might be expected to reduce the feeding and growth opportunities of subordinates. In order to deal with this situation, foraging and growth models need to be spatially explicit. Recent developments in drift-foraging models, two-dimensional habitat models, and individual-based bioenergetics models lay the foundation for this approach (Hughes 1992b, 1998; Clark and Rose 1997; Hardy 1998).

Modeling Growth without Prey Density Estimates

Our study provides support for the generality of Elliott's energetics equations (Elliott 1972, 1975b, 1975c, 1976b). Preall and Ringler (1989) also constructed a bioenergetics model for brown trout from Elliott's equations, but their model does not include prey density nor does it account for reproduction costs. Preall and Ringler used their model to calculate a ratio of observed specific growth rate to predicted maximum growth rate, assuming maximum rations, which they termed the ecological growth coefficient. Our model can be used in the same manner as Preall and Ringler's model when estimates of prey density are unavailable but when data are available on observed growth.

Our study demonstrates that growth limitation is most likely to occur in larger fish once they begin incurring reproductive costs coupled with increasing foraging costs. By including reproduction costs, our bioenergetics model allows growth to be predicted over the lifetime of the fish; our model allows researchers to overcome the size and age limitation of Preall and Ringler's model and of the temperature-based model for growth of brown trout on maximum rations of Elliott et al. (1995). However, it needs to be acknowledged that when the model is used in this manner, Elliott's energetics equations must be extrapolated far beyond the size range of fish upon which they were developed (300 g).

When run on maximum rations and with appropriate options chosen for the foraging model, our bioenergetics model can also be used to predict the growth of trout in lakes. For this application, velocity shear options are omitted, and the trout are assumed to swim at their optimal swimming speed (cf. Kerr 1971; Stewart 1980; Hewett and Johnson 1992; Rand et al. 1993). Energy density of the prey can also be varied for this application in order to accommodate trout that are feeding on invertebrates or fish (cf. Hewett and Johnson 1992).

Research and Management Implications

Bioenergetics models are attractive because they provide a way to link fish growth with causative physical variables and lower trophic levels. They allow the functional responses of fish to be modeled, thus promising a better understanding of how and why growth is influenced by altered physical and prey conditions than is possible with correlative models. Our bioenergetics model has potential for the exploration of growth-limiting factors and associated use as an environmental-impact tool and as an aid for hypothesis generation in studies of fish growth processes in rivers. The strength of the model lies in its ability to integrate physical and food regimes over the lifetime of trout through the medium of growth as well as in the fact that it allows for comparisons of growth trajectories. The model can be used to infer the degree to which growth may be limited by the quantity and quality of the invertebrate food supply within the physiological constraints set by water temperature. For example, it can be used to explore the potential energetic consequences that changes to the taxonomic and size structure of invertebrate communities (such as those that occur with agricultural land use and pollution) will have on trout growth. Other applications include quantifying the impact on trout growth of changes to the thermal regime and clarity of rivers (current versions of the model include water clarity in the prey reaction distance function). We have recently used the model in the above contexts to infer migratory life history patterns and the impact of agriculture on growth potential of trout in New Zealand rivers (Young and Hayes 1999). Components of the brown trout drift-feeding model and those of other bioenergetics models can also assist in investigations of the flow requirements of salmonids. They can demonstrate the functional relationships that underpin fish behavior and the energetic basis of microhabitat and macrohabitat selection (Smith and Li 1983; Hughes 1992b, 1998; Addley 1993; Hughes and Reynolds 1994; Ludlow and Hardy 1996; Braaten et al. 1997).

Bioenergetics applications are now commonplace in the literature. Those dealing with salmonids mainly use the Hewett and Johnson (1992) model, but they also include the various drift-feeding–salmonid models mentioned above. Field tests of these models are rare, mainly because they are expensive (Hewett and Johnson 1992), and this shortcoming has been recognized as a priority for future bioenergetics research (Hansen et al. 1993). Our study has gone some way to meeting that need. More corroboration is needed between measured and predicted growth, ideally in a range of habitats covering the extremes of food and temperature (Hansen et al. 1993; Filbert and Hawkins 1995). The reasonable fit of our model predictions to observed growth is encouraging for the impetus it gives to extending salmonid bioenergetics into energetics-based carrying capacity and population-dynamics models (cf. Clark and Rose 1997). Nevertheless, our model would benefit by further testing, especially in rivers with low drift densities, where foraging energetics should play an even more significant role in limiting growth than was the case in the Maruia River.

The bioenergetics model described in this paper has been programmed as an EXCEL Visual Basic macro. Data input and output is managed via an EXCEL spreadsheet. Copies of the program are available from the senior author.

Acknowledgments

This study was funded by the Foundation for Research, Science and Technology (contract number CAW404, CAW502) and by Fish and Game New Zealand. We appreciated the field and laboratory assistance provided by Yvonne Stark, Krystyna Ponikla, Aaron Quarterman, Susan Hallas, and Tony Hewitt. We also thank David Baird for statistical advice and Roger Young, Nick Hughes, James Hall, and three anonymous for constructive criticism of the draft manuscript. Water-temperature and flow data were provided by Envirolink and the National Institute of Water and Atmospheric Research.

References

Addley, R. C. 1993. A mechanistic approach to modeling habitat needs of drift-feeding salmonids. Master's thesis. Utah State University, Logan.

Allen, K. R. 1969. Limitations on production of salmonid populations in streams. Pages 3–20 *in* T. G. Northcote, editor. Symposium on salmon and trout in streams. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver.

Bachman, R. A. 1982. A growth model for drift-feeding salmonids: a selective pressure for migration. Pages 128–135 *in* E. L. Bannon and E. O. Salo, editors. Proceedings of the salmon and trout migratory behaviour symposium. University of Washington, Seattle.

Bachman, R. A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Transactions of the American Fisheries Society 113: 1–32.

Bachman, R. A. 1991. Brown trout. Pages 208–229 *in* J. Stolz and J. Schnell, editors. Trout. The wildlife series. Stackpole Books, Harrisburg, Pennsylvania.

Backiel, T., and E. D. Le Cren. 1978. Some density relationships for fish population parameters. Pages 279–302 *in* S. Gerking, editor. Ecology of freshwater fish production. Blackwell Scientific Publications, Oxford, United Kingdom.

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

Behnke, R. J. 1992. Native trout of western North America. American Fisheries Society, Monograph 6, Bethesda, Maryland.

Binns, N. A., and F. M. Eiserman. 1979. Quantification of fluvial trout habitat in Wyoming. Transactions of the American Fisheries Society 108:215–228.

Bovee, K. D. 1982. A guide to stream habitat analysis using the instream flow incremental methodology. U.S. Fish and Wildlife Service Biological Services Program FWS/OBS-82/26, Fort Collins, Colorado.

Braaten, P. J., P. D. Dey, and T. C. Annear. 1997. Development and evaluation of bioenergetic-based habitat suitability criteria for trout. Regulated Rivers 13:345–356.

Breck, J. E. 1993. Foraging theory and piscivorous fish: are forage fish just big zooplankton? Transactions of the American Fisheries Society 122:902–911.

Brett, J. R., and N. R. Glass. 1973. Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*). Journal of the Fisheries Research Board of Canada 22:1492–1501.

Brittain, J. E., and T. J. Eikeland. 1988. Invertebrate drift—a review. Hydrobiologia 166:77–93.

Campbell, R. F., and J. H. Neuner. 1985. Seasonal and diurnal shifts in habitat utilized by resident rainbow trout in western Washington Cascade Mountain streams. Pages 39–48 *in* R. H. Hamre, editor. Symposium on small hydropower and fisheries. American Fisheries Society, Bethesda, Maryland.

Chaston, I. 1969. Seasonal activity and feeding pattern of brown trout (*Salmo trutta*) in a Dartmoor stream in relation to availability of food. Journal of the Fisheries Research Board of Canada 26:2165–2171.

Clapp, D. F., and R. D. Clark, Jr. 1990. Range, activity, and habitat of large, free-ranging brown trout in a Michigan stream. Transactions of the American Fisheries Society 119:1022–1034.

Clark, M. E., and K. A. Rose. 1997. Individual-based model of stream resident rainbow trout and brook char: model description, corroboration, and effects of sympatry and spawning season. Ecological Modelling 94:157–175.

Crow, M. E. 1981. Lack of time limitation in fish foraging. Pages 47–55 *in* G. M. Cailliet and C. A. Simenstad, editors. Gutshop '81: fish food habitats studies. Proceedings of the third Pacific workshop. University of Washington, Washington Sea Grant Publication, Seattle.

Cummins, K. W., and J. C. Wuycheck. 1971. Calorific equivalents for investigations in ecological energetics. Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen 18:1–158.

Dunbrack, R. L., L. M. Dill. 1983. A model of size dependent surface feeding in a stream salmonid. Environmental Biology of Fishes 8:203–216.

Edmundson, E., F. H. Everest, and D. W. Chapman. 1968. Permanence of station in juvenile chinook salmon and steelhead trout. Journal of the Fisheries Research Board of Canada 25:1453–1464.

Elliott, J. M. 1967. Invertebrate drift in a Dartmoor stream. Archiv für Hydrobiologie 63:202–237.

Elliott, J. M. 1970. Diel changes in invertebrate drift and the food of trout *Salmo trutta* L. Journal of Fish Biology 2:161–165.

Elliott, J. M. 1972. Rates of gastric evacuation in brown trout, *Salmo trutta* L. Freshwater Biology 2:1–18.

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

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

Elliott, J. M. 1975c. Weight of food required to satiate brown trout, *Salmo trutta*. Freshwater Biology 5: 51–64.

Elliott, J. M. 1976a. Body composition of brown trout (*Salmo trutta* L.) in relation to temperature and ration size. Journal of Animal Ecology 45:273–289.

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

Elliott, J. M. 1994. Quantitative ecology of the brown trout. Oxford University Press, Oxford, UK.

Elliott, J. M., M. A. Hurley, and R. J. Fryer. 1995. A new, improved growth model for brown trout, *Salmo trutta*. Functional Ecology 9:290–298.

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

Fausch, K. D. 1991. Trout as predator. Pages 65–72 *in* J. Stolz and J. Schnell, editors. Trout. The wildlife series. Stackpole Books, Harrisburg, Pennsylvania.

Feldmeth, C. R., and T. M. Jenkins. 1973. An estimate of energy expenditure by rainbow trout (*Salmo gairdneri*) in a small mountain stream. Journal of the Fisheries Research Board of Canada 30:1755–1759.

Field-Dodgson, M. S. 1985. A simple and efficient drift sampler. New Zealand Journal of Marine and Freshwater Research 19:167–172.

Filbert, R. B., and C. P. Hawkins. 1995. Variation in condition of rainbow trout in relation to food, temperature, and individual length in the Green River, Utah. Transactions of the American Fisheries Society 124:824–835.

Glova, G. J., and P. M. Sagar. 1991. Dietary and spatial overlap between stream populations of a native and two introduced fish species in New Zealand. Australian Journal of Marine and Freshwater Research 42:423–433.

Hansen, M. J., D. Boisclair, S. B. Brandt, S. W. Hewett, J. F. Kitchell, M. C. Lucas, and J. J. Ney. 1993. Applications of bioenergetics models to fish ecology and management: where do we go from here? Transactions of the American Fisheries Society 122: 1019–1030.

Hardy, T. B. 1998. The future of habitat modeling and instream flow assessment techniques. Regulated Rivers: Research and Management 14:405–420.

Hayes, J. W. 1996. Bioenergetics model for drift-feeding brown trout. Pages 465–476 *in* M. Leclerc, H. Capra, S. Valentin, A. Boudreault, and Y. Cote, editors. Ecohydraulics 2000: 2nd international symposium on habitat hydraulics, volume B. Institut national de la Recherche scientific—Eau, Quebec City, Quebec.

Hayes, J. W., and D. B. Baird. 1994. Estimating relative abundance of juvenile brown trout in rivers by underwater census and electrofishing. New Zealand Marine and Freshwater Research 28:243–254.

Hayes, J. W., and I. G. Jowett. 1994. Microhabitat use by large brown trout in three New Zealand rivers. North American Journal of Fisheries Management 14:710–725.

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

Henderson, M. A., and T. G. Northcote. 1985. Visual prey detection and foraging in sympatric cutthroat trout (*Salmo clarki clarki*) and Dolly Varden (*Salvelinus malma*). Canadian Journal of Fisheries and Aquatic Sciences 42:785–790.

Hewett, S. W., and B. L. Johnson. 1992. Fish bioenergetics model 2. University of Wisconsin, Sea Grant Institute, Technical Report WIS-SG-92-250, Madison.

Hughes, N. F. 1991. The behavioral ecology of Arctic grayling distribution in interior Alaskan streams. Doctoral dissertation. University of Alaska, Fairbanks.

Hughes, N. F. 1992a. Ranking of feeding positions by drift-feeding Arctic grayling (*Thymallus arcticus*) in dominance hierarchies. Canadian Journal of Fisheries and Aquatic Sciences 49:1994–1998

Hughes, N. F. 1992b. Selection of positions by drift-feeding salmonids in dominance hierarchies: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. Canadian Journal of Fisheries and Aquatic Sciences 49:1999–2008.

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

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

Hughes, N. F., and J. B. Reynolds. 1994. Why do Arctic grayling (*Thymallus arcticus*) get bigger as you go upstream? Canadian Journal of Fisheries and Aquatic Sciences 51:2154–2163.

Jenkins, T. M., Jr. 1969a. Night feeding of brown and rainbow trout in an experimental stream channel. Journal of the Fisheries Research Board of Canada 26:3275–3278.

Jenkins, T. M., Jr. 1969b. Social structure, position choice and micro-distribution of two trout species (*Salmo trutta* and *Salmo gairdneri*) resident in mountain streams. Animal Behaviour Monographs 2:57–123.

Jones, D. R., J. W. Kiceniuk, and O. S. Bamford. 1974. Evaluation of swimming performance of several fish species from the MacKenzie River. Journal of the Fisheries Research Board of Canada 31:1641–1647.

Jowett, I. G. 1992. Models of the abundance of large brown trout in New Zealand rivers. North American Journal of Fisheries Management 12:417–432.

Kerr, S. B. 1971. A simulation model of lake trout growth. Journal of the Fisheries Research Board of Canada 28:815–819.

Lien, L. 1978. The energy budget of the brown trout population of Øvre Heimdalsvatn. Holarctic Ecology 1:279–300.

Ludlow, J., and T. B. Hardy. 1996. Comparative evaluation of suitability curve based habitat modeling and a mechanistic based bioenergetic model using two-dimensional hydraulic simulations in a natural river system. Pages 519–530 *in* M. Leclerc, H. Capra, S. Valentin, A. Boudreault, and Y. Cote, editors. Ecohydraulics 2000: 2nd international symposium on habitat hydraulics, volume B. Institut national de la Recherche scientifique—Eau, Quebec City, Quebec.

Mathur, D. W., E. J. Purdy, and C. A. Silver. 1985. A critique of the instream flow incremental methodology. Canadian Journal of Fisheries and Aquatic Sciences 42:825–831.

McCarter, N. H. 1986. Food and energy in the diet of brown and rainbow trout from Lake Benmore, New Zealand. New Zealand Journal of Marine and Freshwater Research 20:551–559.

McLay, C. L. 1968. A study of drift in the Kakanui

River, New Zealand. Australian Journal of Marine and Freshwater Research 19:139–149.

Messick, C. F. 1995. Response of brown trout to streamflow, temperature, and habitat restoration in a degraded stream. Rivers 5:75–95.

Nehring, R. B., and R. M. Anderson. 1993. Determination of population-limiting salmonid critical habitats in Colorado streams using the physical habitat simulation system. Rivers 4:1–19.

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

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

Preall, R. J., and N. H. Ringler. 1989. Comparison of actual and potential growth rates of brown trout (*Salmo trutta*) in natural streams based on bioenergetic models. Canadian Journal of Fisheries and Aquatic Sciences 46:1067–1076.

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

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

Rice, A., and P. A. Cochran. 1984. Independent evaluation of a bioenergetics model for largemouth bass. Ecology 65:732–739.

Ricker, W. E. 1979. Growth rates and models. Pages 677–743 *in* W. S. Hoar, D. J. Randall, and J. R. Brett, editors. Fish physiology, volume 8. Academic Press, New York.

Ringler, N. H. 1979. Selective predation by drift-feeding brown trout (*Salmo trutta*). Journal of the Fisheries Research Board of Canada 36:392–403.

Robinson, F. W., and J. C. Tash. 1979. Feeding by Arizona trout (*Salmo opache*) and brown trout (*Salmo trutta*) at different light intensities. Environmental Biology of Fishes 4:363–368.

Sagar, P. M., and G. J. Glova. 1987. Prey preferences of a riverine population of juvenile chinook salmon, *Oncorhynchus tshawytscha*. Journal of Fish Biology 31:661–673.

Sage, R. D. 1982. Wet and dry-weight estimates of insects and spiders based on length. American Midland Naturalist 108:407–411.

Sample, B. E., R. J. Cooper, R. D. Greer, and R. C. Whitmore. 1993. Estimation of insect biomass by length and width. American Midland Naturalist 129: 234–240.

Shirvell, C. S., and R. G. Dungey. 1983. Micro-habitats chosen by brown trout for feeding and spawning in rivers. Transactions of the American Fisheries Society 112:355–367.

Smith, J. J., and H. W. Li. 1983. Energetic factors influencing foraging tactics of juvenile steelhead trout *Salmo gairdneri*. Pages 173–180 *in* D. L. G. Noakes, editor. Predators and prey in fishes. Dr. W. Junk, The Hague, Netherlands.

Stewart, D. J. 1980. Salmonid predators and their forage base in Lake Michigan: a bioenergetics-modeling synthesis. Doctoral dissertation. University of Wisconsin, Madison.

Stewart, D. J., J. F. Kitchell, and L. B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. Transactions of the American Fisheries Society 110:751–763.

Towers, D. J., I. M. Henderson, and C. J. Veltman. 1994. Predicting dry weight of New Zealand aquatic macroinvertebrates from linear dimensions. New Zealand Journal of Marine and Freshwater Research 28: 159–166.

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

Wankowski, J. W. J. 1979. Morphological limitations, prey size selectivity, and growth response of juvenile Atlantic salmon *Salmo salar*. Journal of Fish Biology 14:89–100.

Wankowski, J. W. J. 1981. Behavioural aspects of predation by juvenile Atlantic salmon (*Salmo salar* L.) on particulate drifting prey. Animal Behaviour 29: 557–571.

Ware, D. M. 1972. Predation by rainbow trout (*Salmo gairdneri*): the influence of hunger, prey density, and prey size. Journal of the Fisheries Research Board of Canada 29:1193–1201.

Waters, T. F. 1972. The drift of stream insects. Annual Review of Entomology 17:253–272.

Wooton, R. J. 1985. Energetics of reproduction. Pages 231–254 *in* P. Tytler and P. Calow, editors. Fish energetics: new perspectives. Croom and Helm, Beckenham, U.K.

Young, M. K., R. B. Rader, and T. A. Belish. 1997a. Influence of macroinvertebrate drift and light on the activity and movement of Colorado River cutthroat trout. Transactions of the American Fisheries Society 126:428–437.

Young, M. K., R. A. Wilkison, J. M. Phelps, and J. S. Griffith. 1997b. Contrasting movement and activity of large brown trout and rainbow trout in Silver Creek, Idaho. Great Basin Naturalist 57:238–244.

Young, R. G., and J. W. Hayes. 1999. Trout energetics and effects of agricultural land use on the Pomahaka trout fishery. Cawthron Institute, Cawthron Report 455, Nelson, New Zealand.

Appendix follows

Appendix: Constants for Equations in Table 2

TABLE A.1—Constants for C_{max} (from Elliott 1976b: Table 2).

Temperature (°C)	a	b_1	b_2
<6.6	2.902	0.762	0.418
6.6–13.3	15.018	0.759	0.171
13.3–17.8	26.433	0.767	0.126
>17.8	3.214×10^7	0.753	−0.662

TABLE A.2—Constants for F and U for the temperature range 3.8–20.4°C (from Elliott 1976b: Table 2).

Parameter	a	b_1	b_2
F	0.212	−0.222	0.631
U	0.026	0.580	−0.299

TABLE A.3—Constants for R_s, R_{max} (from Elliott (1976b: Table 2)), and SC (in Rand et al. 1993 and Stewart 1980, from Rao 1968). (b_3 is used only in SC.)

Temperature (°C)	Parameter	a	b_1	b_2	b_3
3.8–7.1	R_s and SC	4.126	0.734	0.192	2.34
7.1–19.5	R_s and SC	8.277	0.731	0.094	2.34
3.8–17.8	R_{max}	3.890	0.770	0.204	
17.8–19.5	R_{max}	2.215×10^7	0.757	−0.663	
19.5–21.7	R_{max}	28.833	0.756	0.0325	

TABLE A.4—Constants for maximum meal size (Q) (from Elliott (1975c: Table 3).

Temperature (°C)	a	b_1	b_2
3.8–6.6	0.88	0.762	0.315
6.6–13.3	2.89	0.759	0.133
13.3–18.4	15.55	0.767	0.007
18.4–21.6	3.56×10^7	0.733	−0.785