Development of a Bioenergetics Model for Appalachian Brook Trout

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Abstract: In many Appalachian headwater streams brook trout (*Salvelinus fontinalis)* are the only fish species present. Land use practices or global warming can have a significant effect on the production and survival of brook trout in these streams. Managers must be able to evaluate the potential impact of thermal changes upon these streams and bioenergetics models represent a valuable tool in this effort. Here we present a bioenergetics model for brook trout and conduct a laboratory validation of the model. Model validation experiments showed the model to adequately predict the growth, final weight, and consumption of fish in the experiments. Growth and final weight were estimated within –1.4% (not significantly different than 0) and consumption was slightly underestimated, within –19.7% (± 7.5%) of observed values. Scope for growth from the bioenergetics model suggests that given unlimited food, growth of brook trout may be possible over the range of environmental temperatures supporting brook trout. However, under more restricted rations typical of Appalachian headwater streams (20% *ad libitum*) only modest growth is possible between 3.5 and 20C. These growth restrictions may have serious implications for thermal alterations upon Appalachian brook trout and may suggest that energetically, over winter may be a critical time for these fish.

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Brook trout *(Salvelinus fontinalis)* are the only native salmonid found in inland streams east of the Mississippi River (Meehan and Bjornn 1991). Local residents fish for brook trout for food. Further, because brook trout are native, they are highly prized by many catch-and-release anglers. Brook trout are often found in headwater streams in the Appalachians. These small streams can be greatly influenced by land use practices such as timber harvest and road building that can increase water temperatures and fine sediment that may affect growth, survival, and reproduction of brook trout (Hakala 2000). Of particular importance may be increases in stream water temperatures. Brook trout are a cool water species and generally are not found in systems that exceed 20C for extended periods (Power 1980). Because of these thermal tolerances, climatic warming may compromise brook trout growth and survival. However, despite the widespread importance of brook trout there does not presently exist a means of evaluating the impact climatic warming or altered thermal regimes from deforestation may have upon brook trout.

Bioenergetics models have become popular tools for fisheries managers interested in estimating consumption by fish (Kitchell et al. 1977, Hartman and Margraf 1992, Ney 1993) or for evaluating potential stocking strategies (Stewart et al. 1981, Jones et al. 1993, LaBar 1993). These models can also be used to evaluate the potential impacts of altered thermal regimes upon growth or consumption of fish (Hill and Magnuson 1990, Wildhaber and Crowder 1990). It is in this latter capacity where bioenergetics models may play an important role in assessing streams at risk due to thermal limitations. Many streams presently support brook trout in the Appalachians, but many may become unsuitable if global climatic warming (GCW) raises water temperatures even slightly. A bioenergetics model for brook trout would supply a much needed tool to assess the thermal limits of streams for brook trout and, with thermal data, could be applied spatially to determine which streams are at risk due to GCW in a region. A brook trout bioenergetics model would also be a valuable tool for fisheries managers and biologists interested in studying consumption of this species in the wild and the model could be modified for aquaculture applications. Given the importance of brook trout in the Appalachian region and the value that a bioenergetics model for that species would have for managers, the objective of this study was to develop and test a bioenergetics model for brook trout.

Methods

Model Development

Bioenergetics models are based upon the balanced energy equation described by Winberg (1956):

$$C = G - (M + SDA) - F - U$$

Where C is consumption, G is growth, M is metabolism, SDA is specific dynamic action, F is egestion, and U is excretion. Sensitivity analyses of bioenergetics models have shown the models to be relatively insensitive to the SDA, F, and U parameters (Bartell et al. 1986). Greatest effort should therefore be expended upon determining parameters for consumption and metabolism, which were developed in this study through a series of laboratory experiments. Parameters for SDA, F, and U were borrowed from those reported for brown trout *(Salmo trutta)* by Elliott (1976*a, b*) and widely used to model energetic components for many species of salmonids (Hansen et al. 1997).

Brook trout used in experiments were obtained from the West Virginia Division of Natural Resources Bowden State Fish Hatchery in Elkins, W.Va. during spring 2000 and 2001. These fish are from a hatchery stock that has been captive for over 40 years (M. Shingleton, W. Va. Div. Nat. Resour., pers. commun.). Brook trout were held in living stream tanks in the Fisheries Laboratory at West Virginia University until experiments were begun. During acclimation and holding, fish were fed both dry commercial pellets and housefly larvae. For several days prior to consumption experiments, fish were fed only housefly larvae to prepare them for experimental conditions.

Consumption Experiments

Consumption experiments were conducted using a repeated measures design. Previous research has shown temperature and fish size to be the dominant influences on maximum consumption rates (Cmax) so we considered each of these as independent variables in the design (Hartman and Brandt 1995*b,* Kitchell et al. 1977, Rice et al. 1983, Stewart and Binkowski 1986). In the repeated measures, each fish was tested a maximum of one time per experimental temperature. Experiments were conducted at 6, 8, 13, 16, 21, and 24 C. Temperature treatments were not randomized, but generally reflected natural seasonal temperatures. Fish ranged in size from 6.2 to 22.2 g for temperature-dependence experiments. A size-dependence experiment was conducted with 15 fish ranging in size from 8.2 to 119.8 g at a single water temperature (12.6 C).

Fish were acclimated to each test temperature for a period of at least 21 days prior to experimentation. Fish were then fasted for 24 hours, anesthetized in a clove oil solution of 1.2 ml clove oil dissolved in 12 ml of ethanol per 20 liters of water (Anderson et al. 1997) and weighed (± 0.1 g). Fish were individually placed into temperature-controlled, 38-liter tanks and fed housefly larvae.

An excess of prey were offered to the trout with the excess being removed 24 hours later. Weight of larvae consumed was estimated based upon the number of maggots eaten and the mean weight of maggots offered. After removal of uneaten food, new food was offered and the process repeated. Weight range of maggots within a feeding varied by less than 10% and was considered unimportant in estimating mass consumed during a day. Maximum consumption experiment duration was 7 days. Fish were re-weighed at the conclusion of the experiments to measure growth over the experiment.

Metabolism Experiments

Metabolism experiments were conducted under the same acclimation conditions as for consumption experiments and were done either immediately before, or after the Cmax experiments. Prior to beginning a metabolism experiment fish were fasted for 24–48 hours (longer times for colder temperatures) to eliminate any apparent specific dynamic action from the oxygen consumption measurements (Adams and Breck 1990). Fish were anesthetized and weighed as above and placed individually into 3.0-liter Fernback flasks. The flasks were masked in black plastic to eliminate visual stimuli from other fish or human activity in the laboratory. Fish were acclimated to these metabolism chambers for 24 hours with a continuous flow of water through the chamber to ensure adequate water quality.

Experiments began by completely filling each chamber with water and then measuring the dissolved oxygen concentration in each chamber using a YSI model 58 meter (air-calibrated at the beginning of each day). Each chamber was then sealed with a rubber stopper and the fish were allowed to respire in the closed chamber for a period of time. This time varied with each temperature, but the target was the period of time needed for dissolved oxygen concentration to decline by more than 1 mg/liter. Times to achieve this level of oxygen depletion ranged from 0.5 to 3.5 hours and were longer at colder temperatures.

Once a metabolism experiment began, 3 measures of metabolism were made during the next 24 hours and the average was used as the value of metabolism for each fish. Experiments were conducted at 5.5, 9.5, 12.5, 16, 21, and 24 C. Fish ranged in size from 4.4–26.6 g. Another set of experiments was conducted at 16 C that included fish ranging in size from 4.8–131.2 g to determine the size-dependence of metabolism. Because fish were able to move in the chambers, this measure of metabolism is considered a routine rate (Adams and Breck 1990). Oxygen consumption estimates were converted to energy units using the oxycalorific equivalent value of 13,556 joules/g O_2 (Elliott and Davison 1975).

Model Development/Model Parameters

When all the experiments were completed we developed models to predict the consumption rate and metabolism of brook trout as functions of temperature and size. We used specific rates of metabolism (g O_2/g/d) or consumption (g/g/d) as the dependent variables and size as independent variables in regression models to determine size-dependency. Once size-dependence factors were established we transformed all data to that of a common size (1 g) and then fit models to the temperature-dependence data.

We used the Thornton and Lessem (1978) algorithm, described as equation 3 in the Wisconsin bioenergetics software (Hansen et al. 1997), to fit an equation to the relationship between temperature and maximum consumption (Table 1). This model uses the product of 2 functions to fit the increasing and decreasing limbs of the dome-shaped function. Metabolism data was handled as for consumption with size-dependence relationships calculated through linear regression after log10 transformation. After standardizing the metabolism data to a 1-g fish the temperature-dependence was fit by using the Kitchell et al. model (1974), which is described as equation 2 in the Wisconsin software (Hansen et al. 1997) (Table 1). The metabolism measures used in this study were routine rates, including activity by the fish. For that reason, we assumed the activity multiplier of metabolism (ACT) to be 1 in the metabolism model. All model components are identified in Table 1.

Laboratory Tests of the Model

Before proceeding to field tests of any bioenergetics model it has been suggested that the model be tested in the laboratory under more controlled conditions (Hansen et al. 1993). Therefore we used independent laboratory data in which individual fish were held in flow-thru 38-liter tanks to compare model results with laboratory measures of consumption and growth. Fish were fed several times per day and uneaten food was recovered to estimate consumption. Growth was measured as the difference between weights taken at the beginning and end of an experiment. Experiments lasted 7 days and were conducted at 11.6–15.2 C. At the end of validation ex-

Table 1. Model functions, sources, and parameters for the bioenergetics model for brook trout. Model parameters for each sub-model (consumption, metabolism, egestion, excretion) are listed as they would appear if entered into the Hansen et al. (1997), Fish Bioenergetics 3.0 software. The source provided for each model used to describe an energetic function.

Consumption model (Thornton and Lessem 1978)

Model form:

$Cmax=CA\cdot W^{CB}\cdot f(T)$

where;

Cmax is the maximum specific consumption rate in g food/g fish/day;
CA is the intercept of the allometric mass function;
CB is the slope of the allometric mass function;
W is fish mass in g;
f(T) is the temperature dependence function:

$f(T)=K_A\cdot K_B$

$K_A=(CK1\cdot L1)/(1+CK1\cdot (L1-1))$
$L1=e^{(G1\cdot (T-CQ))}$
$G1=(1/(CTO-CQ))\cdot \ln((0.98\cdot (1-CK1))/(CK1\cdot 0.02))$
$K_B=(CK4\cdot L2)/(1+CK4\cdot (L2-1))$
$L2=e^{(G2\cdot (CTL-T))}$
$G2=(1/(CTL-CTM))\cdot \ln((0.98\cdot (1-CK4))/(CK4\cdot 0.02))$

where;

CQ is the lower water temperature at which the temperature dependence is a small fraction (CK1) of the maximum rate and CTO is the water temperature corresponding to 0.98 of the maximum consumption rate.

CTM is the water temperature (>CTO) at which dependence is still 0.98 of the maximum rate and CTL is the temperature where dependence is a fraction (CK4) of maximum.

Model Values:

CA	0.3103
CB	–0.3055
CQ	7.274
CTO	20.90
CTM	21.00
CTL	24.05
CK1	0.500
CK4	0.203

Respiration model (Kitchell et al. 1974)

Model form:

$R=RA\cdot W\cdot f(T)\cdot ACT$
$S=SDA\cdot (C-F)$

where;

R	Specific rate of respiration (g/g/d)
W	fish weight (g)
RA	Intercept of the allometric mass function (g/g/d)
RB	Slope of the allometric mass function.
f(T)	Function for temperature dependence of respiration.
T	Water temperature (C)
ACT	Multiplier for activity component of respiration.
S	Proportion of assimilated energy lost through specific dynamic action.

Table 1 (continued)

SDA	Specific dynamic action.
C	Specific consumption rate (g/g/d)
F	Specific egestion rate (g/g/d)

$f(\mathrm{T})=\mathrm{V}^{\mathrm{X}}\cdot e^{(\mathrm{X}\cdot(1-\mathrm{V}))}$

$\mathrm{V}=(\mathrm{RTM}-\mathrm{T})/(\mathrm{RTM}-\mathrm{RTO})$

$\mathrm{X}=(\mathrm{Z}_2\cdot(1+(1+40/\mathrm{Y})^{0.5})^2)/400$

$\mathrm{Z}=\mathrm{Ln}(\mathrm{RQ})\cdot(\mathrm{RTM}-\mathrm{RTO})$

$\mathrm{Y}=\mathrm{Ln}(\mathrm{RQ})\cdot(\mathrm{RTM}-\mathrm{RTO}+2)$

where;

RTO is the temperature where respiration is highest.
RTM is the maximum or lethal temperature (C)
RQ is an approximation of the Q10 rate over low water temperatures

Model Values:

RA	0.0085
RB	–0.223
RQ	5.5
RTO	22
RTM	25
ACT	1
SDA	0.172

Egestion and Excretion models (Elliott 1976)

Model form:

$\mathrm{F}=\mathrm{FA}\cdot\mathrm{T}^{\mathrm{FB}}\cdot e^{(\mathrm{FG}\cdot p)}\cdot\mathrm{C}$

$\mathrm{U}=\mathrm{UA}\cdot\mathrm{T}^{\mathrm{UB}}\cdot e^{(\mathrm{UG}\cdot p)}\cdot(\mathrm{C}-\mathrm{F})$

where;

F = egestion (g/g/d)
U = excretion (g/g/d)
FA is the intercept of the proportion of consumed energy egested versus water temperature (T, C) and ration (C, g/g/d).
FB is the water temperature dependence coefficient of egestion
FG is the coefficient of feeding level dependence of egestion.
UA, UB, and UG are similarly defined for excretion.
p is the proportion of maximum consumption (*P* value) for the input conditions (calculated by the software in Hansen et al. (1997))

Model values:

FA	0.212
FB	–0.222
FG	0.631
UA	0.0314
UB	0.58
UG	–0.299

Energy Content Values (joules/g)

Lab Experiments:		*Field Values for Scope for Growth:*	
Brook trout	6473.5	Brook trout	4317
Fly larvae (prey)	8424.6	Prey	4000

periments fish were euthanized in an excess of MS-222 and oven dried to a constant weight at 80 C. The percent dry weight was then used in the Salmonidae energy density equation in Hartman and Brandt (1995*a*) to obtain estimates of energy content for each fish. Energy content of the maggots was obtained from the literature (Cummins and Wuycheck 1971). These energy estimates for predators and prey were used in converting mass to energy units in the bioenergetics models for validation comparisons. A total of 16 single-fish experiments were conducted and used in the laboratory model validation. Fish in these experiments ranged in initial size from 4.6 to 32.8 g with a mean of 18.1 g. The laboratory validation was made based upon the percent error between predicted and observed values of consumption, growth, or final weight from these experiments (Hartman and Brandt 1993, Ney 1993).

Scope for Growth

A graphical analysis of scope for growth was conducted under *ad libitum* and 20% of *ad libitum* rations to evaluate growth capacity of brook trout under different thermal conditions. Scope for growth (Kitchell et al. 1974) graphically depicts the energy budget of a fish over the range of temperatures under which it may occur and depicts energy costs and growth (by difference between consumption and costs) possible at any given temperature. Brook trout scope for growth was calculated over a range of temperatures from 1 to 25 C for a 10-g fish. Age structure of brook trout in headwater streams is typically comprised of primarily age-0 to age-2 fish. A 10-g brook trout would be representative of a fish in the middle of this demographic, typically age-1 in West Virginia streams. In scope for growth analysis we used energy density values of typical prey (Plecoptera, Ephemeroptera, Trichoptera) from Cummins and Wuycheck (1971) of 4000 joules/g. Energy density of brook trout was 4,317 joules/g, derived from the Salmonidae energy density equation (Hartman and Brandt 1995*a*) and yearly average of seasonal percent dry weight data for field collected brook trout (J. Sweka, unpubl. data).

Results

Energetics Experiments and Model Development

Experiments conducted over a wide range of sizes at an average of 12.6 C found specific consumption to decline with increasing fish weight (Fig. 1) with the size-dependent exponent of weight being –0.3055 (r^2=0.64, $P < 0.01$). That exponent was very close to that found for the closely-related lake trout, *(Salvelinus namaycush)* (Stewart et al. 1983) so we felt justified in using our exponent (–0.3055) to standardize our Cmax data to that of a 1-g fish for evaluation of temperature-effects.

The most common use of fisheries bioenergetics models is through the use of the Wisconsin Bioenergetics Model software (Hansen et al. 1997) available through Wisconsin Sea Grant. This model is readily available to managers and biologists, but includes only an exponential model function or 2 dome-shaped models for temperature functions in consumption or metabolism data. Our consumption data included a total of 40 consumption estimates over the range of test temperatures. All tempera-

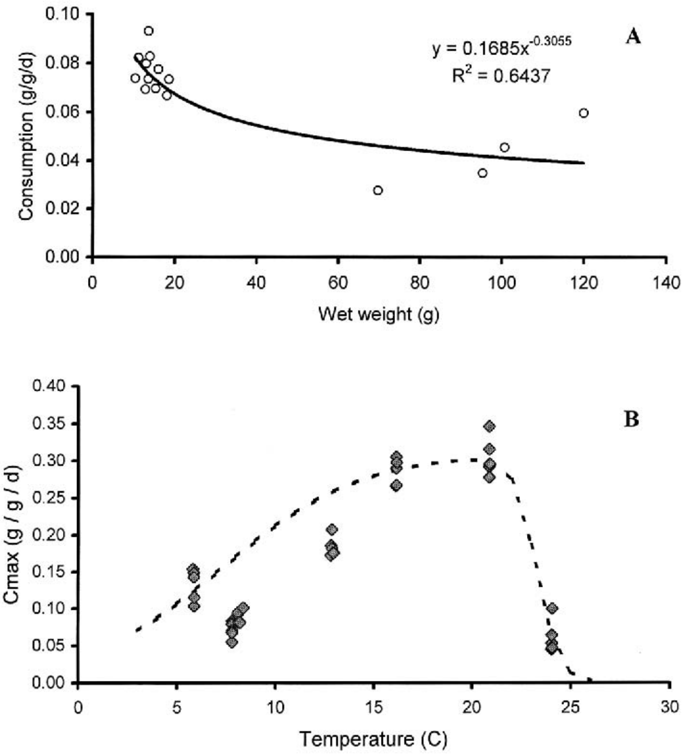

Figure 1. Size–dependence of Maximum Consumption (Cmax) (Panel A) and temperature–dependence of Cmax (Panel B) for brook trout from laboratory experiments. The Thornton and Lessem (1978) model was fit to the data (dashed line), providing a better fit than statistical models.

tures had at least 5 consumption measures and 10 were measured at 8 C. Consumption rate increased rapidly with temperature from 8 to 21 C, then declined rapidly (Fig. 1). This rapid decline made it impossible to fit a statistical exponential model to the data. Therefore we used the Thornton and Lessem (1978) algorithm to describe the effects of temperature upon Cmax (Table 1). This algorithm did a reasonable job of describing the Cmax data (Fig. 1). Because the Cmax function represents the maximum rate (and many factors such as stress or disease may serve to reduce consumption rates while very few factors would account for an anomalously high value), we chose to fit the Cmax model to the higher ration levels observed at 5.5 C rather than the lower rates at 8 and 13 C.

Specific metabolic rate (g O_2 / g / d) increased with temperature and declined with fish size (Fig. 2, Table 1). Our 78 observations were over a range of fish sizes from 4.4 to 26.6 g and temperatures from 5.15 to 23.45 C. As with the consumption data, fitting of an exponential model did not result in a normal distribution of residu-

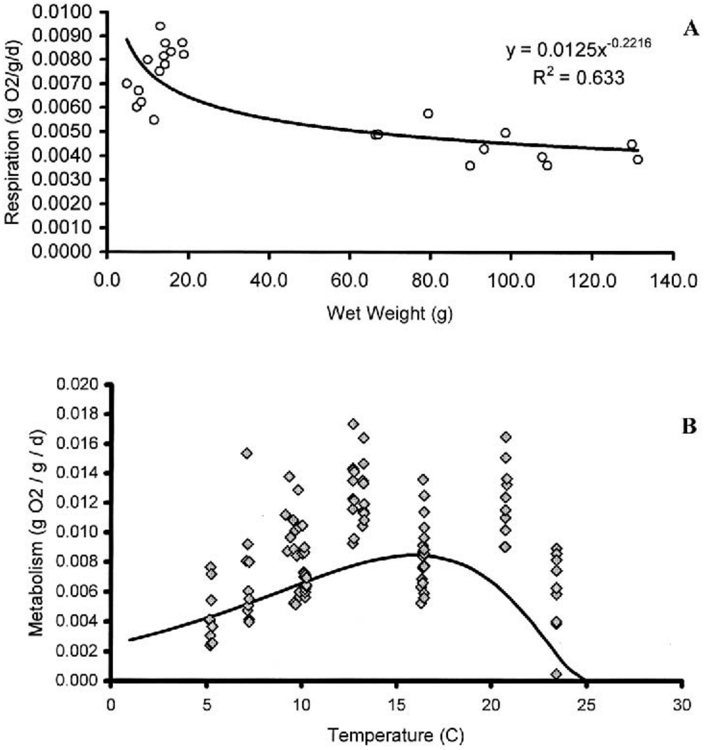

Figure 2. Size–dependence (Panel A) and temperature–dependence (Panel B) of specific metabolism of brook trout at temperatures between 5 and 24 C. In Panel B, all data have been transformed to that of a 1-g fish using the size–dependent exponent of RB in Table 1. The solid line represents the fit of the Kitchell et al. (1974) model to the metabolism data (see Table 1 for equations and values).

als. Metabolism appeared to decrease at upper temperatures (Fig. 2), so we were forced to use the Kitchell et al. (1974) model to describe temperature effects upon metabolism (Table 1). Size-dependence of metabolism was evaluated at the optimum temperature of 16.5 C. The model describing size-dependence was:

$$\text{Met.}(\text{g O}_2 / \text{g} / \text{d}) = 0.0125\ W^{-0.2216} \quad (1)$$

where W is the wet weight of the fish and T is temperature (Table 1). This model was significant ($P < 0.001$) and explained 63% of the variability in the data (Fig. 2).

Laboratory Validation

Validation of the brook trout bioenergetics model with 16 experiments showed the model did a good job of predicting growth, final weight, and consumption. The final weight of trout was underestimated by 1.0% (±3.0%, 95% confidence limits).

Growth rate of trout was underestimated by 1.4% (±11.4%). Consumption rate was underestimated by 19.7% (±7.5%). Thus, there was no significant difference between predicted and observed growth and final weight, but consumption was slightly underestimated.

Scope for Growth

The scope for growth of a 10-g Appalachian brook trout suggests that growth is possible over a wide range of temperatures (Fig. 3). Under *ad libitum* feeding, growth is possible between 1 and 23 C, but is highest between 10–18 C. However, most fish in the wild do not eat at the maximum rate. Generally wild fish eat at a range of 20–50% of Cmax (Hansen et al. 1997) and wild brook trout eat at the lower end of this range (Sweka and Hartman 2001). Given this limitation, and imposing a 20% of maximum ration, the model predicts that very low growth is possible from 4 to 20 C, but at temperatures above 20 C most fish will lose energy.

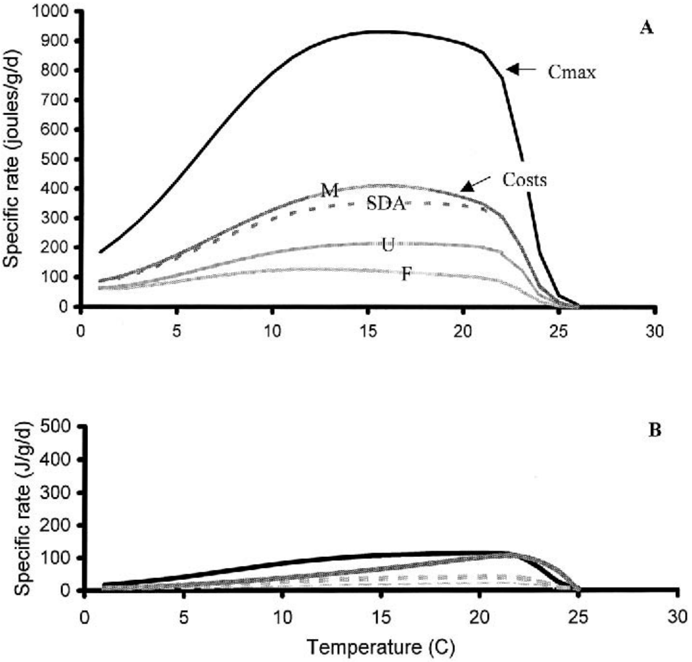

Figure 3. Scope for growth for a 10–g brook trout. Potential growth is identified as the difference between consumption (dashed line is Cmax) and total energetic costs and losses (solid line) at any given temperature. The additive costs of each energetics component are given by U (excretion), F (egestion), SDA (specific dynamic action), and M (metabolism). Panel A represents scope for growth under *ad libitum* feeding and Panel B represents scope for growth under 20% of *ad libitum* feeding conditions that may be more typical of those experienced by wild fish.

Discussion

The brook trout model developed and tested in this study appears to be a robust tool for estimating the consumption and weights attained by brook trout in a laboratory setting. Model validations in the lab were well within the 30–50% error rates suggested by Ney (1993) as being the criteria for utility of bioenergetics models for management applications. Here, the models were within –20% of measured consumption, which would place this evaluation among the best for bioenergetics model validations in general (Ney 1993). Validations for growth and final weight were even better and predictions were not significantly different than measured values. The results of the laboratory validation suggest this model is suitable for use as a tool in management and ecology of wild fish.

The scope for growth estimates that were derived from this study suggest that brook trout may be particularly sensitive to changes in thermal regime. However, this model suggests brook trout may be more tolerant of warm temperatures than earlier reported. Power (1980) reported that the upper lethal temperature for brook trout of the size used here was 25.3 C. However, the preferred temperature range was believed to be between 10–12 C (Power 1980). Our model suggests a similar upper lethal limit, but suggests that the optimum temperature range for growth covers a somewhat wider range (10–19 C) than reported as preferred by brook trout by Power (1980). Further, given unlimited food brook trout appear capable of growing over the range of environmental temperatures in which they can live. Metabolic costs of brook trout are very low compared to most other species and this is the major reason why brook trout are capable of growth at these temperatures. The very low ration levels observed by Sweka and Hartman (2001) of 0.2–0.8% of body weight per day during fall and winter in wild fish represent less than 4% of Cmax at these temperatures and suggest that brook trout are food limited in Appalachian headwater streams.

Based upon scope for growth, brook trout growth was restricted to temperatures less than 24 C. However, the metabolism model (Fig. 2) falls well below observed routine metabolism measures at 21 C, suggesting higher activity rates by brook trout at these temperatures. This higher metabolism at 21 C and above, may be in response to potentially stressful temperatures whereby fish increase their activity in an effort to swim to more favorable environmental conditions. Because the bioenergetics model software is limited to a single activity multiplier we could not account for this change in activity at elevated temperatures in the software. Thus, the scope for growth suggested for brook trout in this model shows growth possible between 21 and 24 C when in fact higher activity rates may make growth impossible at these temperatures. This is supported in fish growth observed in the consumption experiments at 24.1 C where 5 of 11 fish gained weight and 6 of 11 fish lost weight. Mean growth was 0.0017 g/g/g at 24.1 C. For streams that attain maximum summer temperatures of close to 21 C, any land-use impacts or alterations in global climate that slightly increase the water temperatures could prove devastating without thermal refugia.

The brook trout model presented in this study will provide a valuable first step in evaluating the ecological energetics of brook trout in the Appalachians. The model can likely be improved by gathering additional data and validation experiments for a wider range of fish sizes. However, most brook trout in Appalachian streams are of sizes similar to those used in these experiments (Hakala 2000). Further research is needed, and underway to define energy losses through egestion and specific dynamic action for brook trout as well as to define standard metabolism of brook trout. These parameters will be important in defining future models for brook trout; however, the model presented here is suitable for many applications in the region.

One utility of this model will be to suggest to managers in what systems brook trout may be imperiled due to thermal regime alterations. These thermal alterations may come from changes in land use practices such as surface mining or logging activities or through global climatic warming (Brown and Krygier 1970, Hogg et al. 1995). With advances in technology, temperature data loggers have become inexpensive and can provide the thermal history information necessary to obtain site-specific water temperature data on a continuous basis over large geographic regions. This information can be used in conjunction with this bioenergetics model in a GIS format to predict the impacts of thermal changes on larger geographic scales (e.g., Brandt 1993).

The bioenergetics model presented here can also have use to biologists wishing to evaluate the consumptive demand of brook trout in Appalachian streams. Bioenergetics models have been widely used to estimate consumption of wild fish from measures of growth and other site-specific data (Kitchell et al. 1977, Hartman and Brandt 1995*c*, Hansen et al. 1997). Bioenergetics models have also been used in conjunction with data or assumptions on prey availability to evaluate stocking or to examine the utility of introducing fish into new systems (Stewart et al. 1981, Jones et al. 1993) or to evaluate habitat suitability from the fish's perspective (Brandt et al.1992, Goyke and Brandt 1993). Development of this bioenergetics model is only the first step in understanding the interactive role of physiology and environment upon management and biology of fishes in Appalachian headwater streams.

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