

## APPLICATION OF A BIOENERGETICS MODEL FOR BROWN TROUT TO EVALUATE GROWTH IN SOUTHEAST MINNESOTA STREAMS<sup>1</sup>

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*Abstract.*—We examined the influence of water temperature, diet, and feeding sites on growth differences of brown trout *Salmo trutta* in southeast Minnesota streams. Streams were classified as having either fast or slow growth based on back-calculated lengths at age and incremental growth measurements from scales collected in 2002 and 2003. Mean back-calculated lengths at age in fast-growth streams exceeded 141 mm at age 1, 229 mm at age 2, and 289 mm at age 3. In slow-growth streams, mean back-calculated lengths did not exceed 127 mm at age 1, 208 mm at age 2, and 268 mm at age 3. The frequency of feeding sites was low in both stream groups, although possibly higher in the fast-growth streams. Water temperatures were significantly warmer in the fast-growth streams in summer and somewhat cooler in winter. We used a Wisconsin-style bioenergetics model for brown trout to independently test the effects of water temperature and diet, holding other parameters constant. Differences in temperature regime alone were not sufficient to explain differences in growth, and, in fact, predicted slower growth in the fast-growth streams in summer. Different diets resulted in differing predicted weight gains when temperature was held constant; diets with the highest energy densities always resulted in the greatest predicted weight gains. For younger cohorts, diet items with high energy densities included amphipods and mayflies (Ephemeroptera). Estimated consumption rates increased with summer temperatures. Our data suggested that growth differences among streams were likely due to differences in diet and prey availability, with more energy-rich diets available in fast-growth streams. We hypothesize that differences in diet and prey availability are mediated by water temperatures.

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## Introduction

Brown trout *Salmo trutta* are a recreationally important fish in southeast Minnesota and growth varies among streams there (MNDNR 1997). Catching a large brown trout (i.e., > 16 inches, 406 mm) is at least moderately important to 47% and very important to 20% of anglers (Vlaming and Fulton 2003). Modeling results indicate that abundance of large brown trout should be greater in streams with faster than average growth (MNDNR 1997). Consequently, identification of factors promoting faster growth can aid management for larger brown trout. External factors influencing salmonid growth include feeding habitat space (Fausch 1984), water temperature (Lobón-Cerviá and Rincón 1998; Nicola and Almodóvar 2004), and composition and availability of prey (Hinz and Wiley 1998).

Feeding-habitat space can influence growth as some drift-feeding salmonids, including brown trout, compete for stream locations, termed feeding sites, that maximize access to drifting prey while minimizing energy expended for swimming (Bachman 1984; Fausch 1984). As feeding sites become more abundant, more individuals will be able to grow faster (Newman 1993).

Kwak (1993) suggested that trout growth was likely to be more limited in streams with cooler water temperatures in southeast Minnesota. Thorn et al. (1997) suggested that conservation practices of the 1930s-1950s increased infiltration and flow in many streams, resulting in increased area of coldwater habitat. The presence of more cold water in some stream reaches may have decreased temperatures below the optimum for brown trout growth, reported as 12.6-15.4 °C by Bachman (1991). Preall and Ringler (1989) determined that water temperature was the dominant feature governing brown trout growth in New York streams because growth rates of age 1 and older fish were consistently about 60-90% of the maximum possible rate, given the observed temperature regimes in several streams.

Alternatively, others have suggested that trout growth differences among streams

may be related to differences in diet composition and prey availability. Amphipods are an important prey item for smaller and younger trout, especially in streams with luxuriant growths of aquatic vegetation (Waters 1982; Newman and Waters 1984; Bachman 1991). Amphipod abundance was positively related to trout biomass (mostly brown trout) in southeast Minnesota streams (Kwak 1993). Brown trout larger than about 300 mm total length (TL) consume mostly fish, with young trout, sculpins, minnows, darters, and lampreys being most prevalent (Becker 1983). Sculpin *Cottus* spp. may be a preferred prey in southeast Minnesota streams even when other species such as white sucker *Catostomus commersoni* are available (Dineen 1947). Although trout and white sucker are available prey, their growth rates may preclude their importance as a year-round diet item. Amphipods and sculpins have higher energy densities than most other prey types, but their distribution and abundance varies among southeast Minnesota streams (Muck and Newman 1992; Thorn and Anderson 1999). This spatial variability has been attributed to agricultural chemicals and habitat disturbances (Muck and Newman 1992; Thorn and Anderson 1999). Preall and Ringler (1989) listed numerous studies that associated brown trout growth with other environmental variables such as alkalinity, trout density, and gradient. They suggested these environmental variables indirectly influenced trout growth through effects on food availability. Diet and temperature regime interact in a complex way to limit trout growth. Bioenergetics models can help disentangle the effects of temperature and diet to explain differences in growth among populations (Hanson et al. 1997; Railsback and Rose 1999; Yako et al. 2000).

This study compares the relative effects of water temperature and diet on growth of brown trout in streams characterized by fast and slow growth, identifies factors affecting food availability by testing relationships between estimated food consumption rate and selected environmental variables, and tests the hypothesis that fast-growth streams have more feeding sites than slow-growth streams.

## Methods

### *Growth rates*

To identify fast- and slow-growth streams, we estimated current growth rates, quantified as length at age and incremental growth, using back-calculation approaches (Busacker et al. 1990). We initially identified 16 streams that had a range of growth rates from historic data (Table 1; MNDNR 1997) and determined slow and fast growth from the 25<sup>th</sup> and 75<sup>th</sup> percentiles. We verified our fast- vs. slow-growth classification of historic data in spring 2002 and 2003. Brown trout were collected by electrofishing and lengths, weights, and scale samples taken to estimate age and growth. We compared the mean back-calculated length at age and mean incremental growth for the age 1, 2, and 3 cohorts between fast- and slow-growth streams for

2002 and 2003 to check whether growth differed significantly during our study period. Mean back-calculated lengths at age and incremental growth were compared with ANOVA. All data were checked for normality prior to analyses.

### *Water temperature*

Water temperatures were obtained from the 16 study streams using electronic thermographs set to record temperature (<sup>o</sup>C) every hour from 1 April 2002 to 30 September 2002 (summer) and from 1 October 2002 to 31 March 2003 (winter). Missing data were estimated from predictive equations developed from data from the nearest stream as in Hinz and Wiley (1998). Temperature measurements were summarized into the following indices: the percent of hours in the optimum

Table 1. Study streams, study site locations (river mile [rmi] and river kilometer [rkm] from mouth; study site lengths [m]), and spring trout densities (#/km) for 16 streams studied to determine factors associated with brown trout growth in 2002 and 2003 in southeast Minnesota.

Stream	Study site locations			Trout density			
	rmi	rkm	Site length	2002		2003	
				Age 1 cohort	Adults	Age 1 cohort	Adults
Slow growth							
Ferguson Creek	0.5	0.8	156	1,586	537	1,388	512
Gribben Creek	1.9	3.1	269	2,203	741	2,861	1,356
Beaver Creek	3.5	5.6	389	1,009	1,848	1,978	1,609
North Branch Creek	2.2	3.5	359	498	1,098	507	1,444
Trout Run Creek	8.7	14.0	284	731	915	1,656	980
Average growth							
East Beaver Creek	0.0	0.0	385	336	856	917	641
South Fork Root River	35.3	56.8	367	596	794	567	1,104
Middle Br. Whitewater R.	2.4	3.8	271	841	3,079	738	1,129
East Indian Creek	7.0	11.3	209	798	440	778	394
West Indian Creek	5.4	8.7	247	1,534	1,543	706	949
Rush Creek	11.6	18.7	313	2,837	805	2,897	873
Cedar Valley Creek	2.5	4.0	256	256	496	843	397
Fast growth							
Hay Creek	10.9	17.5	232	776	818	846	566
Garvin Brook	2.8	4.5	327	4,420	469	1,478	1,349
South Br. Whitewater R.	3.5	5.6	1,231	309	1,279	1,117	1,197
Winnebago Creek	6.0	9.6	330	1,312	1,418	1,274	895

temperature range for growth (12.6-15.4 °C), a monthly mean, and a daily mean. The optimum temperature index was compared between fast- and slow-growth stream classes, and winter and summer seasons with a two-way ANOVA. Monthly mean temperatures were compared between fast- and slow-growth stream classes, and among months with a two-way ANOVA with month as a repeated measures factor. All data were checked for normality prior to analyses. Daily mean water

temperatures were used in bioenergetics model simulations.

#### *Bioenergetics model simulations*

We used the Wisconsin bioenergetics model (Hanson et al. 1997) configured for brown trout (Table 2; Appendix 1) to evaluate the relative roles of water temperature and diet in brown trout growth. To do this we compiled a set of standard parameters for diet

Table 2. Parameter values used to implement the Wisconsin bioenergetics model for various salmonid fishes including parameter estimates proposed for brown trout for this study. Model equations described by Hanson et al. (1997).

Parameter	Sockeye salmon Beauchamp et al. 1989	Coho salmon Stewart and Iberra 1991	Steelhead Rand et al. 1993	Lake trout Stewart et al. 1983	Brown trout
<b>CONSUMPTION</b>					
Equation	3	3	3	1	3
CA	0.303	0.303	0.628	0.0589	0.2161
CB	-0.275	-0.275	-0.3	-0.307	-0.233
CQ	3	5	5	0.1225	3.8
CTO	20	15	20	X	17.5
CTM	20	18	20	X	17.5
CTL	24	24	24	X	20.8
CK1	0.58	0.36	0.33	X	0.23
CK4	0.50	0.01	0.2	X	0.10
<b>RESPIRATION</b>					
Equation	1	1	1	1	1
RA	0.00143	0.00264	0.00264	0.00463	0.0013
RB	-0.209	-0.217	-0.217	-0.295	-0.269
RQ	0.086	0.06818	0.06818	0.059	0.0938
RTO	0.0234, 0.033	0.0234	0.0234	0.0232	0.0234
RTM	0	0	0	0	0
RTL	25	25	25	11	25
RK1	1	1	1	1	1
RK4	0.13	0.13	0.13	0.05	0.13
ACT	9.9	9.7	9.7	11.7	9.7
BACT	0.0405	0.0405	0.0405	0.0405	0.0405
SDA	0.172	0.172	0.172	0.172	0.172
<b>EGESTION/EXCRETION</b>					
Equation	3	3	3	3	3
FA	0.212	0.212	0.212	0.212	0.212
FB	-0.222	-0.222	-0.222	-0.222	-0.222
FG	0.631	0.631	0.631	0.631	0.631
UA	0.0314	0.0314	0.0314	0.0314	0.0314
UB	0.58	0.58	0.58	0.58	0.58
UG	-0.299	-0.299	-0.299	-0.299	-0.299
<b>PREDATOR ENERGY DENSITY</b>					
Equation	2	2	2	2	2
Alpha 1	5233	5764	5764	5701	5591
Beta 1	7.7483	0.9862	0.9862	3.0809	7.7183
Cutoff	196	4000	4000	1472	151
Alpha 2	6647	5674	7602	9092	6582
Beta 2	0.5249	0.9862	0.5266	0.7786	1.1246

composition, prey energy densities, seasonal weight gain, P-values, and water temperatures, as in Yako et al. (2000). The P-value is the proportion of maximum consumption rate at which the fish is feeding, where consumption rate is expressed as grams of prey consumed per gram of fish body mass per day (Hanson et al. 1997). Standardized parameters were either measured in the field or taken from existing sources (Table 3). Standardized starting and ending weights for each cohort and season were the mean weight of each brown trout cohort measured in the field, except for the starting summer weight of age 0 brown trout. We used 0.1 g for this weight based on brown trout fry emergence information in Newman (1985) and Anderson (1983). Body composition of about 10% for invertebrate taxa and 3.3% for fish taxa were considered indigestible (Hanson et al. 1997). Sample size for the age 3 cohort was not sufficient to estimate weight gain over winter. The standard parameters were used for all bioenergetics models unless otherwise noted.

We first examined temperature effects, using the model to predict how much weight a brown trout should gain in each stream's temperature regime, given that trout in each stream all weighed the same initially and were feeding on the same diets at the same rate (i.e., same P-value). Second, we next examined diet composition effects, predicting growth under various diets, while holding initial trout weights and temperatures standard. Third, we estimated stream-specific P-values by fitting the model with stream-specific values for initial weight, final weight, and temperature regime. The bioenergetics model can be applied in these various ways because the underlying structure is simply an energy balance equation. Finally, we isolated consumption effects, using the stream-specific P-values but with standard initial trout weights and a standard temperature regime.

We used the temperature effects models to determine if water temperature regimes would lead to greater predicted weight gain in fast-growth streams in either summer or winter. If the bioenergetics model predicted greater weight gain in fast-growth streams due only to their temperature regimes, this would

support the idea that brown trout growth in southeast Minnesota is regulated by temperature. Predicted weight gains were compared between fast- and slow-growth stream classes and summer and winter seasons with a two-way ANOVA for each cohort.

To identify the relative importance of different forage taxa, hypothetical diets were constructed with varying prey composition. Diet combinations were simply ranked from the diet resulting in the greatest weight gain to the diet resulting in the least weight gain.

To identify environmental factors related to food availability, we took the estimated stream-specific P-values as a surrogate measure of prey composition and availability (Railsback and Rose 1999) and tested relationships between this measure and selected physicochemical and biotic variables. Estimated P-values for each stream should be direct measures of trout consumption rate and hence related to prey composition and availability (Railsback and Rose 1999). We applied linear regression methods to test the relationship between P-values and selected physicochemical and biotic variables suggested by others as modifiers of prey composition and availability: mean and maximum water temperature in summer, trout density, watershed slope, conductivity, stream gradient, mean pool depth, channel width, percent aquatic vegetation, percent silt substrate, percent of the sampling station composed of pool habitat, and percent of the sampling station having feeding sites (McFadden and Cooper 1962; Hynes 1970; Troelstrup 1992; Newman 1993; Railsback and Rose 1999; Greenberg et al. 2001). Population estimates for age 0 and adult trout were made in spring 2002 using catch depletion methods and converted to density estimates (number/km). Watershed slope was measured from maps and GIS data. Conductivity was measured at upstream and downstream ends of each sampling station and averaged. Stream gradient was measured with a laser transit. Remaining variables were measured with a transect method similar to that of Nerbonne and Vondracek (2001) in July and August (i.e., summer low flows) in 2002. Transects were spaced four stream widths apart, and depth, column

Table 3. Standard parameters used for bioenergetics model simulations to predict weight gain of four cohorts of brown trout due to water temperature or diet effects in southeast Minnesota streams from 1 April 2002 to 31 March 2003. Diet proportions based on diet data from Valley Creek, Minnesota (Grant 1999). Prey energy densities for invertebrate taxa were from Cummins and Wuycheck (1971). Salmonidae energy density was from Railsback and Rose (1999). Calculated P-values, the proportion of maximum consumption, were calculated using the bioenergetics model and based on brown trout observed weight gain. The standard parameter for water temperature was the daily mean water temperature averaged over 16 study streams in southeast Minnesota. All simulations were run on a daily time step.

Standard parameters	Cohort			
	Age 0	Age 1	Age 2	Age 3
<b>Diet proportions</b>				
Trichoptera	0.64	0.88	0.88	0.39
Ephemeroptera	0.10			
Amphipoda	0.12	0.03	0.03	0.02
Chironomidae	0.10			
Other invertebrates	0.04	0.03	0.03	0.01
Gastropoda		0.06	0.06	0.06
Salmonidae				0.52
<b>Prey energy density (J/g)</b>				
Trichoptera	2,925	2,925	2,925	2,925
Ephemeroptera	4,705	4,705	4,705	4,705
Amphipoda	4,429	4,429	4,429	4,429
Chironomidae	2,562	2,562	2,562	2,562
Other invertebrates	3,177	3,177	3,177	3,177
Gastropoda	5,273	5,273	5,273	5,273
Salmonidae	5,900	5,900	5,900	5,900
<b>Water temperature effects only</b>				
Summer start/end weight (g)	0.1/16	29/95	123/223	244/374
Summer calculated P-value	0.7103	0.5736	0.5158	0.3173
Winter start/end weight (g)	16/25	95/128	223/261	Insufficient data
Winter calculated P-value	0.4233	0.4783	0.4188	Insufficient data
<b>Diet effects only</b>				
Start/end weight (g)	0.1/25	29/128	123/261	244/374
Calculated P-value	0.6226	0.5439	0.4856	0.3173

velocity, substrate type, presence of aquatic vegetation and presence of adult trout cover were measured or recorded at sampling points located at 1-m intervals along the transect. The first transect began 0.5 stream width upstream from the downstream station boundary. Sampling points began 0.5 m from a randomly selected bank. After the first transect, the starting sampling point alternated between banks. Mean pool depth was the mean of all depths measured in pool habitats. Percent vegetation and silt were the percentage of sampling points having either or both of these characteristics. Mean channel width was the mean of all channel widths measured. Pool length and stream length were measured with a tape measure, and percent pool was calcu-

lated from the length measurements. Each sampling point was classified as a suitable or unsuitable feeding site depending on its depth, velocity, and cover characteristics. We defined optimum feeding sites for brown trout, as depths exceeding 0.3 m with velocities between 0.20 and 0.30 m/s for age 1 and 2 trout and depths exceeding 0.6 m with velocities between 0.15 and 0.29 m/s for age 3 trout (Shirvell and Dungey 1983; Hayes and Jowett 1994; Grant 1999). Cover also had to be present within 1 m of these points.

The stream-specific P-values were checked for normality prior to regression analyses and, if necessary, arc-sine-square-root transformed to meet that assumption (Zar 1984). Independent variables were also

checked for normality, and either log 10 or arc-sine-square-root transformed to facilitate identification and interpretation of more linear relationships (Zar 1984). Univariate linear regression models were developed to identify the variables with the strongest relationship with trout consumption for each of four cohorts - ages 0, 1, 2, and 3. Model development followed the process in Dieterman and Galat (2004). Individual physiochemical and biotic variables significantly related to trout consumption were identified with univariate regressions. Variables not significantly related in univariate models were culled. Pearson correlations were then used to further cull variables and identify a final list of variables most highly correlated with trout consumption, but not highly correlated with each other. All analyses were considered significant if  $P \leq 0.05$ . However, acceptance levels for all tests were adjusted by the sequential Bonferroni correction for multiple tests (Holm 1979; Rice 1989), thereby maintaining experiment-wise error rates at the 0.05 level.

We assessed the relative importance of water temperature vs. food consumption for predicting the observed weight gain with linear regression as in Railsback and Rose (1999). Two regressions were run for each cohort: (1) observed weight gain regressed against weight gain predictions from temperature effects models; and (2) observed weight gain regressed against weight gain predictions from consumption effects models. The only differences are that one set of bioenergetics models was based on stream-specific temperatures with a standard consumption rate, while the other was based on a standard temperature regime with stream-specific P-values. Whichever effect produced the strongest relationship between observed and predicted weight gain (i.e., lowest statistical  $P$ , largest slope coefficient, greatest  $R^2$ ) would be most important.

#### *Feeding sites*

We examined the effect of feeding sites on brown trout growth by estimating the prevalence of feeding sites in each stream and in slow- and fast-growth stream groups with a Bayesian analysis using WinBUGS software (available at <http://www.mrc-bsu.cam.ac.uk/>

[bugs/welcome.shtml](#)). We also examined an estimate of confidence regarding the conclusion that fast-growth streams have a higher prevalence of feeding sites than slow-growth streams. We used a hierarchical model in which the mean prevalence of feeding sites is estimated for each group of streams  $q[j]$  and the stream-specific prevalence estimates  $p[i]$  vary about the group means. More specifically, the  $\text{logit}(p[i])$  values were presumed to be normally distributed about the  $\text{logit}(q[j])$  values with mean 0 and precision  $\tau$ . Uninformative priors were given for  $\text{logit}(q[j])$  and  $\tau$ . Bayesian results provide a better estimate of the prevalence of feeding sites and a more accurate probability statement for those estimates than frequentist statistical procedures, especially when the variable of interest, feeding sites in this instance, is rare. We made independent estimates for the age 1-2 and age 3 cohorts.

## **Results**

### *Growth rates*

Brown trout mean back-calculated length at age varied among streams and between years (Table 4). We found the 35<sup>th</sup> and 65<sup>th</sup> percentiles clearly identified three groups of streams, based on the current back-calculated length-at-age data. The 35<sup>th</sup> percentile of back-calculated lengths at age was 127 mm for age 1, 208 mm for age 2, and 268 mm for age 3. Study streams with back-calculated lengths at age less than these 35<sup>th</sup> percentiles were classified as slow-growth streams. The 65<sup>th</sup> percentiles were 141 mm at age 1, 229 mm at age 2, and 289 mm at age 3. Streams with back-calculated lengths at age greater than these 65<sup>th</sup> percentiles were classified as fast-growth streams. We omitted all streams with intermediate back-calculated lengths at age from subsequent analyses to more clearly contrast factors influencing broad growth differences among streams. Mean back-calculated lengths at age and length increments are listed for the identified growth classes in Table 5. Mean (back calculated) lengths at age were significantly different between fast- and slow-growth streams, but length increments differed only for the age 1 cohort in both years and the age 2 cohort in

Table 4. Mean back-calculated length at age in millimeters (sample size, N) for brown trout in southeast Minnesota streams with slow, average, and fast growth in 2002 and 2003.

Stream	Length at age							
	2002				2003			
	Age 1	2	3	4	1	2	3	4
<i>Slow growth</i>								
Ferguson	97(81)	155(56)	226(25)	309(2)	109(57)	174(37)	243(8)	298(1)
Gribben	114(98)	198(59)	256(21)	290(4)	102(77)	181(55)	256(19)	279(2)
Beaver	110(102)	183(82)	261(24)	273(1)	125(91)	214(57)	279(7)	
North Br.	127(87)	210(62)	274(18)		125(75)	211(45)	278(7)	
Trout Run	119(87)	204(53)	273(9)	317(1)	132(85)	215(55)	266(19)	310(3)
Mean	113	190	258	297	118	199	264	295
<i>Average growth</i>								
East Beaver	131(99)	220(66)	284(30)	331(8)	127(102)	225(61)	281(25)	337(6)
So. Fk. Root <sup>a</sup>	127(86)	220(45)	297(6)	361(3)	137(69)	218(47)	301(9)	
Mid. Br.								
Whitewater <sup>a</sup>	137(82)	215(50)	268(15)		136(83)	216(51)	280(16)	339(3)
East Indian	137(93)	217(58)	290(9)	310(2)	135(66)	229(34)	272(7)	
West Indian	134(105)	218(73)	289(26)	348(3)	130(86)	210(58)	277(13)	327(1)
Rush	143(86)	232(41)	295(10)	385(3)	133(82)	224(45)	285(4)	
Cedar Valley <sup>a</sup>	140(71)	215(42)	275(4)		147(65)	231(33)		
Mean	135	219	285	347	135	222	282	334
<i>Fast growth</i>								
Hay <sup>b</sup>	148(94)	227(54)	284(20)	320(6)	153(82)	240(43)	293(9)	311(2)
Garvin <sup>b</sup>	145(92)	227(55)	280(35)	346(7)	144(93)	237(60)	318(8)	360(2)
So. Br.								
Whitewater	148(108)	227(71)	289(28)	342(15)	151(93)	246(60)	305(8)	
Winnebago Cr.	153(98)	236(63)	301(32)	349(8)	149(92)	250(45)	333(8)	399(2)
Mean	148	229	288	339	149	243	312	356

<sup>a</sup>Formerly classified as a fast-growth stream.

<sup>b</sup>Formerly classified as an average-growth stream.



Table 5. Analysis of variance table comparing the back-calculated mean length at age (mm) and incremental growth in length (mm) of brown trout between southeast Minnesota streams classified as having fast (N=4 streams) and slow (N=5 streams) growth in 2002 and 2003. Growth data were collected in the spring of both years. The Type III SS is appropriate for studies with unbalanced designs (Hatcher and Stepanski 1994).

Year	Mean in fast	Mean in slow	df	Type III SS	F	P
Mean back-calculated length at age 1 = (Incremental growth of age 1)						
2002	149	113	1	2737.800	36.15	<0.001
2003	149	119	1	2087.605	21.68	0.002
Mean back-calculated length at age 2						
2002	229	190	1	3423.472	12.01	0.010
2003	243	199	1	4351.250	18.17	0.004
Mean back-calculated length at age 3						
2002	289	258	1	2067.222	8.19	0.024
2003	312	264	1	5088.050	19.61	0.003
Mean incremental growth of age 2						
2002	77	72	1	53.355	0.82	0.395
2003	88	72	1	523.605	12.14	0.010
Mean incremental growth of age 3						
2002	59	52	1	108.889	1.63	0.242
2003	56	47	1	168.200	1.52	0.257

2003 (Table 5; Figure 1). This implies that most growth differences between fast- and slow-growth streams were established at the earliest ages and were consistent over time.

#### *Water temperature*

The thermal regime differed between fast- and slow-growth streams. Fast-growth streams were significantly warmer in summer and somewhat cooler in winter (Table 6; Figure 2). Temperatures were in the optimum range for brown trout growth an average of 1% of the time in winter and 28% in summer (ANOVA testing the effect of season; df 1,17;  $F = 115.57$ ;  $P \leq 0.05$ ), but the time did not differ significantly between fast- and slow-growth stream classes (ANOVA testing the effect of growth class; df 1,17;  $F = 0.91$ ;  $P = 0.35$ ).

#### *Bioenergetics model simulations*

Models of water temperature effects predicted significantly more weight gain in

summer than in winter (Table 7; Figure 3). Although fast-growth streams were significantly warmer in summer, the bioenergetics model predicted cohorts 1, 2, and 3 to gain significantly less weight in these streams than in slow-growth streams (Figure 3). Predicted weight gain of the age 0 cohort did not differ between fast- and slow-growth streams. There was no significant relationship between observed weight gain and weight gain predicted from water temperatures (Figure 4, left column). Thus, water temperature differences did not explain growth differences in these data.

In all diet composition models, the diet composed of prey items with the greatest energy densities resulted in the greatest model-predicted weight gain (Table 8). For example, increasing proportions of amphipods, with an energy density of 4,429 J/g, in the diet of cohorts 0, 1, and 2 resulted in increased weight gain when the remainder of the diet was composed of other terrestrial and

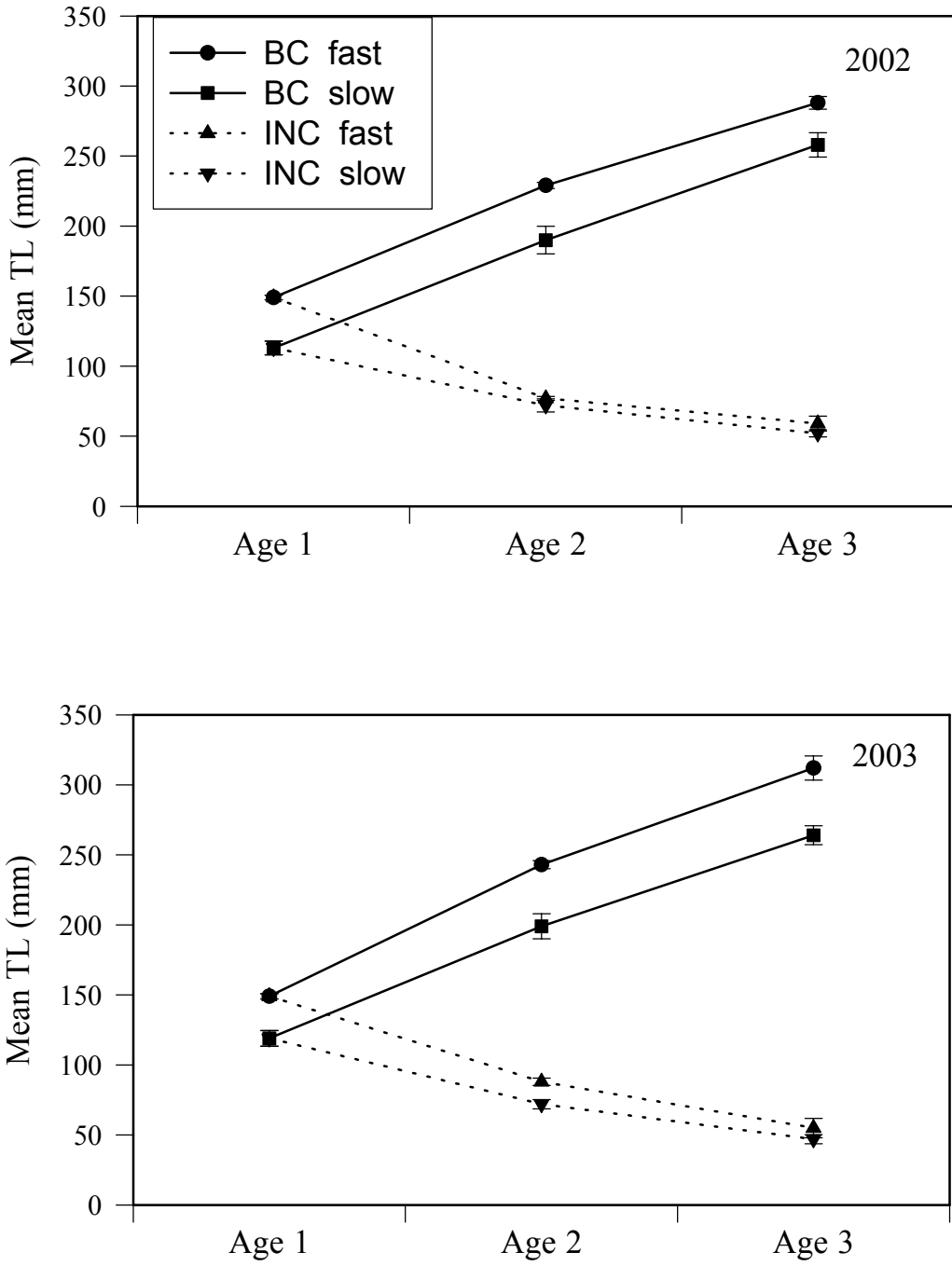


Figure 1. Mean back-calculated length at age (BC; increasing lines) and incremental growth (INC; decreasing lines) measured as TL in mm ( $\pm 1$  SE) in four streams characterized as having fast growth for brown trout and five streams characterized as having slow growth in southeast Minnesota. Growth was measured from scales collected from trout in spring 2002 and 2003.

Table 6. Two-way repeated measures analysis of variance comparing mean water temperature ( $^{\circ}\text{C}$ ) across 12 months and between southeast Minnesota streams classified as having fast ( $N=4$  streams) and slow ( $N=5$  streams) brown trout growth. Month was specified as the repeated measure. Water temperatures were collected hourly from 1 April 2002 to 31 March 2003. A significant growth class X month interaction indicates that the temperature regime in fast- and slow-growth stream classes is different in different months.

Source	df	Type III SS	F	<i>P</i>
Between streams	8	16.47		
Growth class	1	6.76	4.88	0.0629
Residual between	7	9.71		
Within streams	99	1982.52		
Month	11	1805.51	108.16	<0.0001
Growth class X month	11	60.16	3.60	0.0004
Residual within	77	116.85		
Total	107	1998.99		

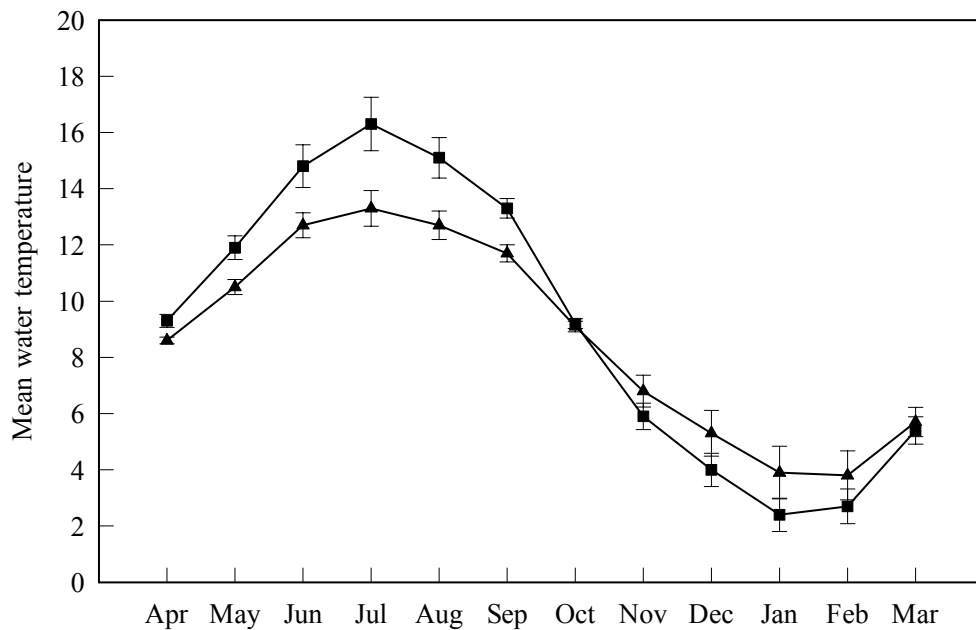


Figure 2. Mean water temperature ( $^{\circ}\text{C}$ ) ( $\pm 1$  SE) in four streams characterized as having fast growth (square symbols) for brown trout and five streams characterized as having slow growth (triangle symbols) in southeast Minnesota, 1 April 2002-31 March 2003.

Table 7. Analysis of variance table comparing bioenergetics model predicted weight gain (g) of four brown trout cohorts due to water temperature effects only. Weight gain comparisons are between southeast Minnesota streams classified as having fast and slow brown trout growth and winter and summer seasons. The bioenergetics model predicted weight gain using mean daily water temperatures measured in fast- and slow-growth streams between 1 April 2002 and 31 March 2003. Diets (Grant 1999) and proportions of maximum consumption (P-values) were held constant for all model simulations. There is no season effect for the age 3 cohort because insufficient numbers of brown trout were collected to estimate weight gain over winter.

Source	df	Type III SS	F	P
Age 0 cohort				
Growth class	1,17	58.081	3.03	0.103
Season	1,17	150.285	7.85	0.014
Growth class X Season	1,17	5.725	0.30	0.593
Age 1 cohort				
Growth class	1,17	1134.225	5.29	0.037
Season	1,17	3809.002	17.77	0.001
Growth class X Season	1,17	1.225	0.01	0.941
Age 2 cohort				
Growth class	1,17	3546.944	7.42	0.016
Season	1,17	14617.877	30.58	<0.001
Growth class X Season	1,17	273.877	0.57	0.461
Age 3 cohort				
Growth class	1,8	7540.138	8.53	0.022

aquatic invertebrates with an energy density of 3,177 J/g. A diet of more Ephemeroptera, Plecoptera, and Trichoptera taxa (EPT; 3,647 J/g) resulted in greater predicted weight gain for the age 1 and 2 cohorts when compared to diets with more Chironomidae (2,742 J/g). More sculpin (5,740 J/g) and trout (5,900 J/g) in age 3 brown trout diets resulted in greater predicted weight gain than diets with white sucker or terrestrial and aquatic invertebrates (Table 8).

Our surrogate measure of prey composition and availability (i.e., stream-specific P-values) was unrelated to most physicochemical conditions and trout densities measured (Table 9) even though many of these variables varied among the 16 study streams (Table 10). Mean and maximum summer water temperatures were the only variables significantly related to P-values for the youngest three cohorts following corrections for multiple tests (Table 9). The P-values of the age 3 cohort were not related to any variable measured. Mean and maximum summer tem-

peratures were correlated with each other (Pearson correlation coefficient  $r = 0.94$ ,  $P \leq 0.0001$ ). Mean water temperature in summer had a greater effect on P-values than maximum temperature because it was more highly related to the P-values for the age 0, 1, and 2 cohorts (Table 9). The slopes of these regressions were 0.076 for the relationship with age 0 consumption, 0.055 for age 1, and 0.044 for age 2 (Figure 5). Thus, in streams with higher mean summer water temperatures, brown trout were able to feed at a higher proportion of maximum consumption rate, and older brown trout were more food limited.

Consumption effects were a better predictor of observed weight gain than temperature effects for all four cohorts. Regressions with consumption effects had steeper slopes and explained more of the variation in observed weight gain than temperature effects (Figure 4).

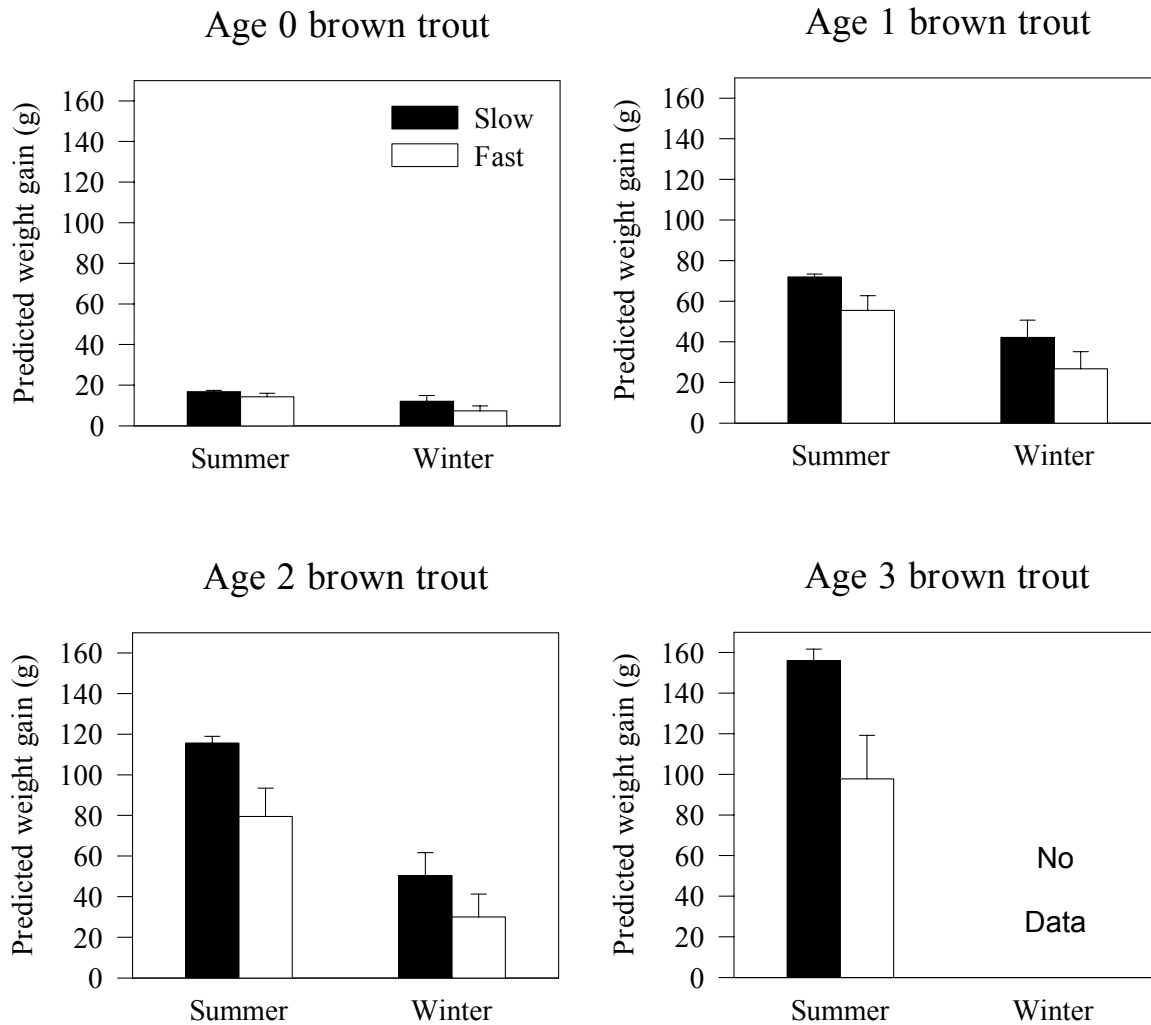


Figure 3. Predicted weight gain of brown trout as influenced by water temperature regimes in streams in southeast Minnesota. Bars show the mean weight gain (g) ( $\pm 1$  SE) of an average brown trout in five slow- and four fast-growth streams examined in this study. Water temperatures were measured 1 April 2002-31 March 2003. All other things being equal, temperature regimes were less favorable to growth in the fast-growth streams.

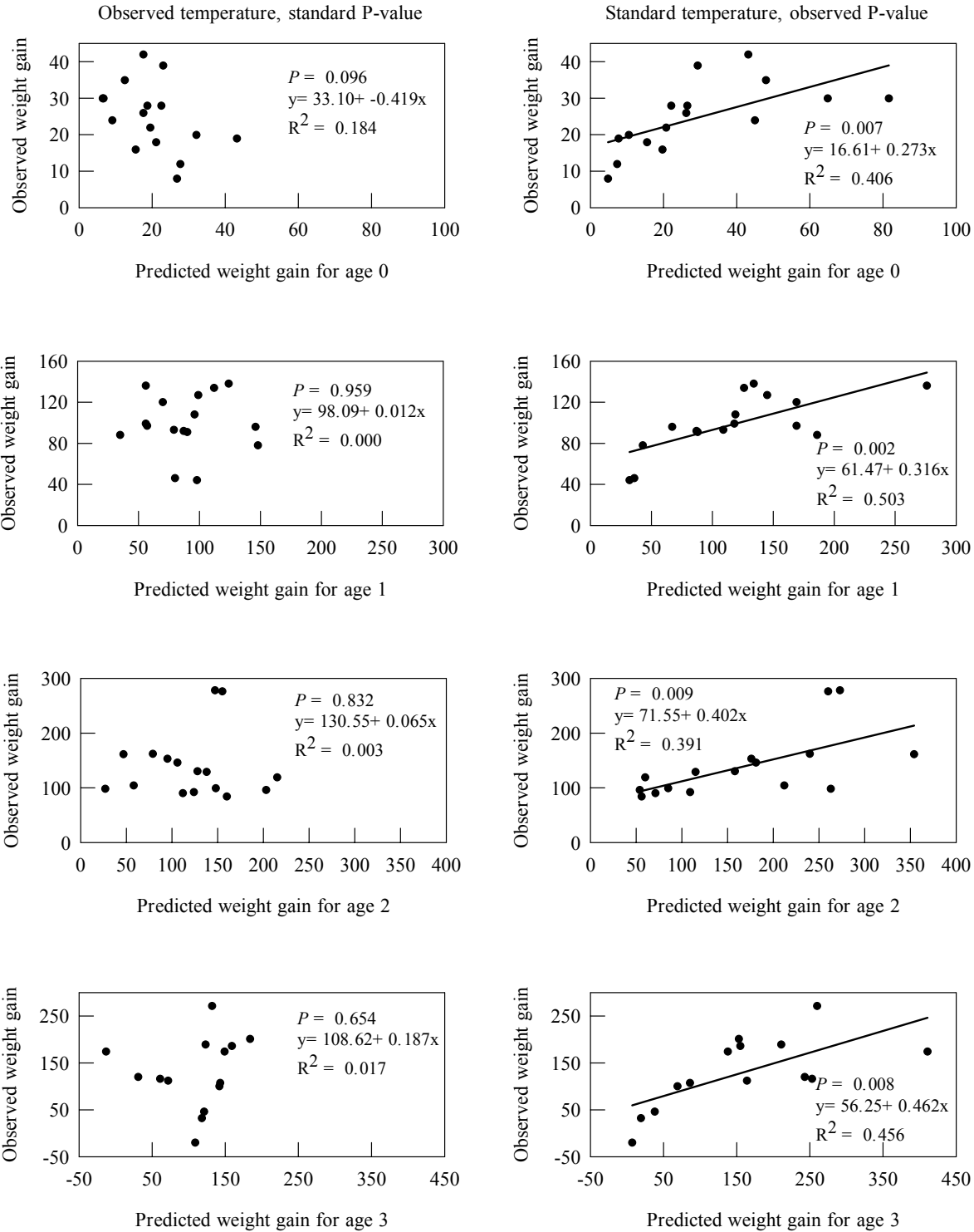


Figure 4. Observed versus predicted weight gain for four brown trout cohorts in 16 streams in southeast Minnesota. The left column shows models with stream-specific temperature regimes, but identical consumption rates (P-value). The right column shows models with stream-specific consumption rates (P-value) but identical temperature regimes. Observed weight gain (g) was the mean weight gain of each cohort between 1 April 2002 and 31 March 2003.

Table 8. Diet combinations and caloric energy values (J/g wet body mass) used to predict weight gain (g) of four brown trout cohorts over one year with the Wisconsin bioenergetics model with brown trout parameters developed in this study. The water temperature regime used in these model simulations was the **average** daily water temperature measured from 16 coldwater streams in southeast Minnesota from 1 April 2002 to 31 March 2003. Simulated diets are presented as ranks from diets producing the most weight gain to those producing the least weight gain.

Diet	Amphipod 4,429 J/g <sup>a</sup>	Other Invertebrates 3,177 J/g <sup>b</sup>	EPT <sup>c</sup> 3,647 J/g	Chironomidae 2,742 J/g <sup>d</sup>	Sculpin 5,740 J/g <sup>e</sup>	Trout 5,900 J/g <sup>f</sup>	White sucker 4,100 J/g <sup>g</sup>	Predicted weight gain (g)
<i>Age 0 brown trout</i>								
1	50%	50%						53
2	25%	75%						35
3	12%	88%						28
4		100%						22
<i>Age 1 and 2 brown trout</i>								
5	20%	80%						<u>age 1</u> 132
6	15%	85%						187
7	10%	90%						125
8	5%	95%						176
9		100%						118
<i>Age 1 and 2 brown trout</i>								
10			100%					111
11			75%	25%				156
12			50%	50%				105
13			25%	75%				147
14				100%				159
<i>Age 3 brown trout</i>								
15						100%		225
16					25%	75%		131
17					50%	50%		186
18					75%	25%		107
19					100%			149
20					75%		25%	85
21		25%			75%			116
22						50%		86
23					50%		50%	
24					25%		75%	
25		50%				50%		
26		50%			50%			
27							100%	
28		75%			25%			
29		50%					50%	
30		100%						

<sup>a</sup>Hanson et al. 1997

<sup>b</sup>Aquatic and terrestrial insects; Cummins and Wuycheck 1971

<sup>c</sup>Ephemeroptera, Plecoptera, and Trichoptera; assumed 33% diet of each and caloric values for each from Cummins and Wuycheck 1971

<sup>d</sup>Cummins and Wuycheck 1971

<sup>e</sup>slimy sculpin; Stewart et al. 1983

<sup>f</sup>Railsback and Rose 1999

<sup>g</sup>estimated from MNDNR file data and data in Hartman and Brandt 1995

Table 9. Probability values for simple linear regressions testing the relationship between the proportion of maximum consumption at which brown trout were feeding and various physicochemical and biotic variables in 16 southeast Minnesota streams. Proportion of maximum consumption (i.e., P-value) was estimated with a Wisconsin bioenergetics model (Hanson et al. 1997) configured for brown trout. Daily water temperatures and annual weight gain of four brown trout cohorts used to run the model were collected from 1 April 2002 to 31 March 2003. Probability values in bold were significant ( $P \leq 0.05$ ) following corrections for multiple tests (Holm 1979; Rice 1989).

Variable	Proportion of maximum consumption model probability			
	Age 0	Age 1	Age 2	Age 3
Mean temperature ( $^{\circ}$ C) in summer	<b>0.0001</b>	<b>0.0001</b>	<b>0.0008</b>	0.0978
Maximum summer temperature ( $^{\circ}$ C)	<b>0.0001</b>	<b>0.0002</b>	<b>0.0014</b>	0.1724
Mean channel width (m)	0.0182	0.0245	0.0962	0.0436
Watershed slope (m/km)	0.0563	0.3099	0.7356	0.2739
Percent aquatic vegetation	0.1000	0.0362	0.4627	0.9981
Stream gradient (m/km)	0.1105	0.2287	0.8675	0.9993
Mean pool depth (cm)	0.1122	0.1089	0.3808	0.0434
Percent silt substrate	0.1887	0.7201	0.4348	0.0881
Density of age 1+ trout (all species)	0.2730	0.1739	0.3138	0.1760
Density of age 0 trout (all species)	0.3060	N/A	N/A	N/A
Percent feeding sites in station— ages 1, 2	N/A <sup>a</sup>	0.4004	0.8172	N/A
Percent feeding sites in station— age 3	N/A	N/A	N/A	0.0048
Percent pool habitat in station	0.6763	0.4480	0.0931	0.3619
Conductivity ( $\mu$ S)	0.7836	0.6690	0.3004	0.3432

<sup>a</sup>N/A – Not an appropriate relationship.

### Feeding sites

Feeding sites for both age 1-2 and age 3 groups were rare in our study streams and composed a relatively low percent of stream area (Table 10). Feeding sites were more prevalent in fast-growth streams than in slow-growth streams (10% vs. 5% for ages 1-2; 3% vs. 2% for age 3). We were 92% confident that there were more feeding sites in fast-growth streams than in slow-growth streams for age 1-2 brown trout, and 80% confident for a similar difference for age 3 trout.

### Discussion

Kwak (1993) and others have noted slower brown trout growth in colder streams in summer in southeast Minnesota. We also found slower growth in streams that were cooler in summer, but our bioenergetics models showed temperature regimes in the fast-growth streams should have been less favorable to growth because summer water temperatures were too warm. The streams supporting the fastest observed growth rates were significantly warmer in the summer and somewhat cooler in winter than streams sup-

porting slow growth rates. We propose that the most important effect of temperature is an indirect one, producing changes in composition and quantity of prey available more than sufficient to offset the greater metabolic costs in the warmer fast-growth streams.

Even though summer water temperatures were warmer in our fast-growth streams than the range for optimal growth, the faster growth would still be possible if brown trout were consuming a more energy-rich diet there. Our consumption-effects model performed better than our temperature-effects model, predicting weight gains more similar to observed weight, and thus supporting the theory that diet was an important determinant of brown trout growth. Incremental growth analyses indicated that growth differences between fast- and slow-growth streams appeared at the youngest ages. Because young trout primarily consume invertebrates (Becker 1983), this suggests that invertebrate communities differ between fast- and slow-growth streams.



Table 10. Physicochemical data for 16 coldwater stream reaches in southeast Minnesota. Mean and maximum water temperatures ( $^{\circ}\text{C}$ ) are from hourly measurements collected between 1 April 2002 and 30 September 2002. Remaining variables were measured during July and August 2002. Cond. is conductivity. Feeding sites for 150-300 mm TL brown trout were sites where depth was  $> 0.3$  m and velocities ranged from 0.20 to 0.30 m/s. Feeding sites for brown trout  $> 300$  mm TL were sites where depth was  $> 0.6$  m and velocities ranged from 0.15 to 0.29 m/s.

Stream	Water temperature		Other physicochemical variables							Percent of reach with brown trout feeding sites		
	Mean water temp.	Max. water temp.	Station gradient (m/km)	Cond. ( $\mu\text{S}$ )	Pool depth (cm)	Channel width (m)	Percent aquatic veg.	Percent silt substrate	Percent pool	Watershed slope (m/km)	Trout ages 1-2	Trout age 3
Ferguson <sup>a</sup>	11.6	18.5	11.84	500	28.7	3.1	61	18	56	19.3	3.9	0.0
Gribben <sup>a</sup>	11.3	18.5	6.49	610	35.3	4.9	50	21	54	24.7	7.9	0.9
Beaver <sup>a</sup>	12.9	19.5	6.26	543	42.5	5.5	20	52	63	25.4	1.5	0.8
North Branch <sup>a</sup>	10.7	14.0	7.52	620	37.4	5.9	77	16	70	7.7	4.7	2.3
Trout Run <sup>a</sup>	12.0	19.0	3.81	595	44.9	9.4	49	38	66	9.5	9.9	4.5
East Beaver	11.1	17.0	4.88	550	47.7	4.9	45	19	77		11.3	5.2
So. Fk. Root River	13.7	23.0	5.14	580	38.5	6.9	46	19	77	9.1	8.1	3.6
Mid. Br. Whitewater	15.0	23.0	5.82	580	55.6	8.2	42	6	57	9.8	10.4	8.7
East Indian	13.7	21.0	2.77	550	42.9	5.7	33	47	82	19.5	2.7	0.0
West Indian	11.6	17.5	2.63	560	50.9	5.3	36	38	81	13.5	5.9	1.2
Rush	14.8	23.5	3.48	550	35.3	7.8	34	19	63	10.4	11.8	5.9
Cedar Valley	14.1	22.3	3.28	500	39.2	4.6	69	17	49		8.7	2.9
Hay Cr. <sup>b</sup>	13.9	21.0	2.37	530	33.8	4.5	41	14	80	10.0	19.2	1.4
Garvin Br. <sup>b</sup>	12.4	19.0	6.83	540	35.1	5.5	66	18	51	23.5	4.5	1.5
So. Br. Whitewater <sup>b</sup>	14.8	24.3	5.31	610	49.0	11.4	13	12	58	6.2	12.9	8.6
Winnebago <sup>b</sup>	13.0	21.0	4.51	510	46.5	7.5	74	27	66	15.3	6.6	1.7

<sup>a</sup> Classified as a slow-growth stream.

<sup>b</sup> Classified as a fast-growth stream.

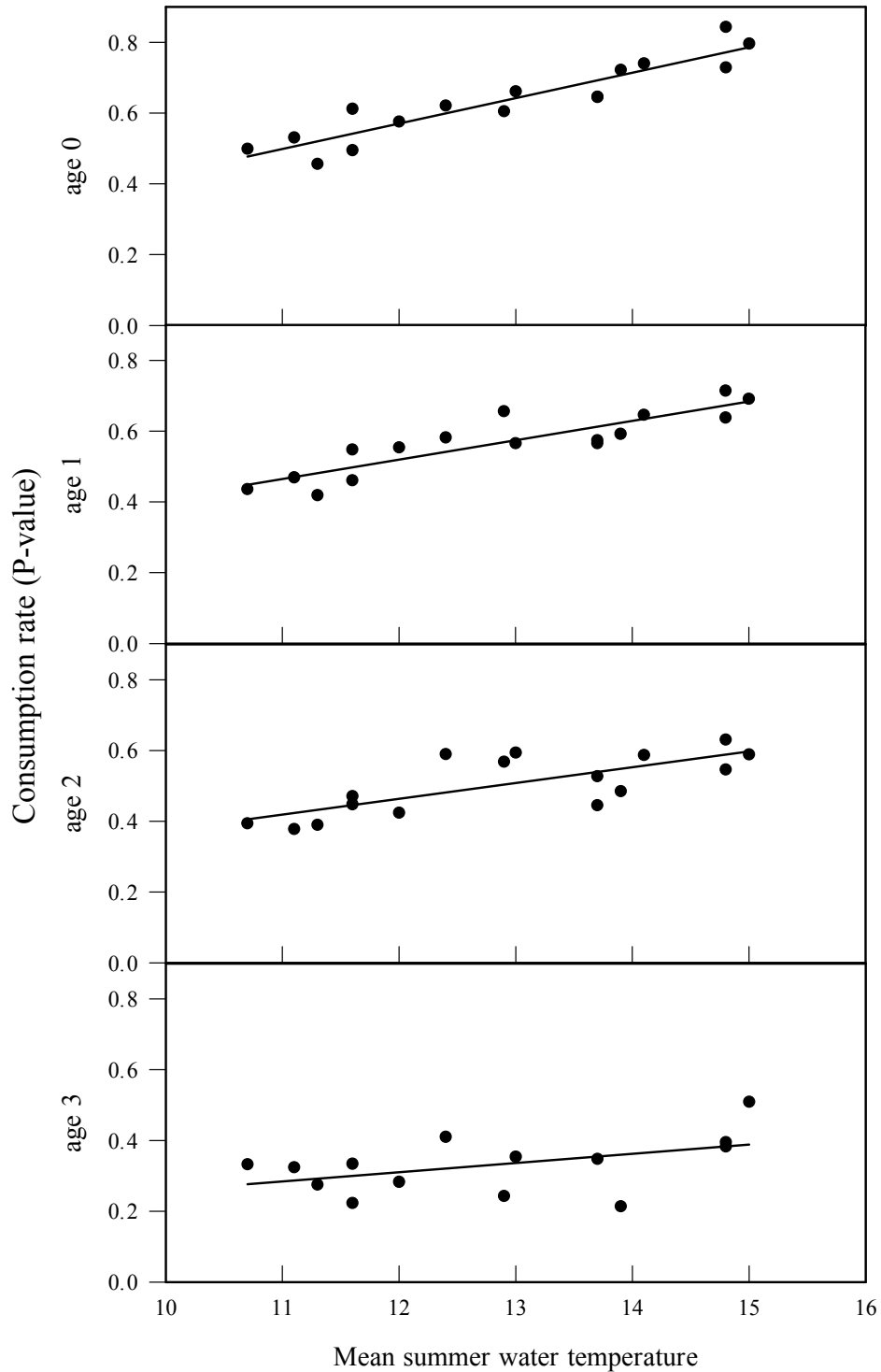


Figure 5. Consumption rate (P-value) over the entire year versus mean summer 2004 water temperature (°C) for four brown trout cohorts in 16 streams in southeast Minnesota. Consumption rate (P-value) was estimated for each stream with a Wisconsin bioenergetics model configured for brown trout (Hanson et al. 1997), a standard diet, stream-specific water temperatures, and stream-specific weight gain between 1 April 2002 and 30 March 2003.

Invertebrate community composition and abundance can be strongly influenced by water temperature (Vannote and Sweeney 1980; Ward and Stanford 1982; Wang and Kanehl 2003). Consequently, differing thermal regimes among our study streams could result in a more energy-rich invertebrate diet in the warmer streams where we observed fast growth. More specifically, Ephemeroptera composed 65% and 70% of the number of invertebrates in kick net samples from two of our fast-growth streams, Garvin Brook and South Branch Whitewater River, respectively (N. Mundahl, Winona State University, personal communication). Conversely, Ephemeroptera composed 16 – 48% of invertebrates in samples from three of our slow-growth streams (N. Mundahl, Winona State University, personal communication). Energy density of Ephemeroptera is 4,705 J/g, and is generally higher than those of most other invertebrates (Table 3). Trichoptera, which have a lower energy density than Ephemeroptera (2,925 J/g; Table 3), composed a higher percent invertebrate composition in three of our slow-growth streams (range 24-46%) than in two of our fast-growth streams (10% and 16%) (N. Mundahl, Winona State University, personal communication). Also, the amphipod taxa *Gammarus* spp. (Amphipoda energy density = 4,429 J/g) was absent from invertebrate collections in our slowest growth stream, Ferguson Creek, in 2000 and 2001 (N. Mundahl, Winona State University, personal communication).

We propose that water temperature differences between fast- and slow-growth streams have important indirect effects on brown trout growth by influencing invertebrate diet composition and prey availability. Similarly, Hinz and Wiley (1998) found juvenile brook trout growth to be significantly related to water temperatures in Michigan rivers. However, water temperatures accounted for only a portion of the growth variation ( $R^2$  ranged from 0.16 to 0.64 depending on temperature variable). Further analyses with a causal path model showed that, although water temperature was the strongest factor affecting variation in juvenile brook trout growth, about one-half of the water temperature effect was

due to its effect on food rations. Biomass of two groups of macroinvertebrates differed among study streams because of temperature differences among the streams. These two macroinvertebrate groups composed the primary food rations affecting brook trout growth. Our results show water temperature had a strong influence on brown trout growth; however, we believe all of its positive effects were due to effects on prey composition and availability. Stream-specific P-values increased with mean summer water temperature for brown trout cohorts 0, 1, and 2 (Table 9; Figure 5), thus as mean summer water temperatures increased the trout were able to feed at a higher proportion of maximum consumption. However, the low P-value estimates, 0.2 - 0.8, showed that the brown trout were not feeding and growing at near maximal rates even in the best streams.

One limitation of modeling temperature or diet composition effects alone is that such models do not account for fish size, and fish size has profound influences on brown trout growth (Elliott 1994; Bond 1996). Our conclusions from those models are limited: warmer temperatures alone do not produce faster growth; and diets with higher energy content allow higher growth. Those models set the stage for models based on observed fish sizes and temperatures to estimate stream-specific P-values. The P-values decreased with age, suggesting a shortage of larger or more energy-rich prey for the larger brown trout.

It is conceivable that our bioenergetics model parameters may not have adequately characterized brown trout physiology in southeast Minnesota streams. Our model parameters were developed from the extensive work on brown trout physiology conducted by Elliott (1994) and Elliott et al. (1995). Elliott's fish originated from brown trout stocks in England at approximate latitude of 54° (Elliott et al. 1995). Based on his results, Elliott developed a bioenergetics model for brown trout (Elliott 1975a; Elliott et al. 1995). This model has subsequently been tested in almost 70 brown trout populations, mostly at higher latitudes in European rivers and lakes (Nicola and Almodóvar 2004). However, the model pre-

dicted slower than observed growth for brown trout populations in warmer Spanish rivers at more southerly, about 40<sup>o</sup>– 43<sup>o</sup>, latitudes (Lobón-Cerviá and Rincón 1998, Nicola and Almodóvar 2004). The authors postulated this discrepancy between the model-predicted and observed growth was due to local physiological adaptations of more southerly brown trout populations to warmer climates. Consequently, brown trout physiology, and hence bioenergetics model parameters, may differ between northerly and southerly populations. Our study streams were located at approximately 43<sup>o</sup> latitude, a more southerly location than the origin of Elliott's fish. Munch and Conover (2002) developed separate bioenergetics model parameters for more northerly, Nova Scotia, and more southerly, South Carolina, populations of Atlantic silversides *Menidia menidia*. Their bioenergetics model parameters differed by an average of 28%. Nicola and Almodóvar (2004) recommended reciprocal transplant experiments to detect local thermal adaptations so more accurate model parameters could be developed. However, such work was beyond the scope of this study. Thus, interpopulation variation in fish physiology is possible, and might cause error in our bioenergetics model parameters. Because brown trout metabolic costs increase as a power function of temperature (Hanson et al. 1997), slower growth must result at warmer temperatures unless food consumption (cal·g<sup>-1</sup>·day<sup>-1</sup>) increases. Small changes in parameters resulting from local adaptation would be unlikely to reverse that relationship or alter our primary conclusion. Although fish size and physiological differences among populations cannot be completely ignored as potential explanations of growth differences in our model simulations, our data suggest that growth differences among streams were primarily due to differences in forage, with water temperature mediating differences in forage composition and availability.

### Management Implications

Because differences in diet composition and prey availability appear to be important determinants of brown trout growth, reintroductions of native forage species could

be considered to increase growth. The distributions of sculpins and amphipods have been reduced by past habitat degradation (Muck and Newman 1992; Thorn and Anderson 1999), but it may be possible to reintroduce them. Native forage assessments could be incorporated into routine fish population assessments to identify candidate streams for reintroduction and potential donor streams. The best candidates would be the colder, slow-growth streams lacking amphipods and sculpin, both energy-rich prey taxa.

Our idea that reintroductions of native forage species could increase brown trout growth rates has not been proven, therefore, such reintroductions should be evaluated to establish cause and effect. Amphipods (*Gammarus* spp.) thrive in colder waters, are an energy rich invertebrate, are common in brown trout diets (Bachmann 1991; Grant 1999), and resulted in good predicted growth of younger trout in our model simulations. Kwak (1993) found that amphipod abundance was positively related to trout biomass (mostly brown trout) in southeast Minnesota. However, we are unsure of their ability to survive in these watersheds with continual use of agricultural chemicals (Muck and Newman 1992). Our models predicted greater weight gain with sculpin diets than with diets composed of most invertebrate taxa or white suckers. However, small trout, which are abundant, should provide at least an equivalent energy density as sculpin. The reintroduction of mottled sculpin *Cottus bairdi* in a Wisconsin stream did not result in any benefits to age 2 and older brown trout (Brynildson and Brynildson 1978), and small brown trout did not exhibit any growth benefits when confined in enclosures with slimy sculpin in a Minnesota stream (Reutz et al. 2003). Cause and effect would be difficult to prove without an experimental evaluation because 30-50% of the variation in invertebrate and fish community structure can be explained by large-scale geologic and geomorphic variables (Wiley et al. 1997; Blann 2004). Therefore, a more detailed field assessment of differences in diet and prey availability between fast- and slow-growth streams would help test the validity of our modeling results.

Prevalence of feeding sites was low in all streams and confounded our ability to detect a difference between fast- and slow-growth groups. Prevalence was somewhat higher in fast-growth streams and suggests a need for additional research or monitoring to clarify the role of this habitat variable. Alternatively, the importance of feeding sites could be tested with instream habitat management projects and subsequent measurement of brown trout growth. Our feeding site definitions incorporated a combination of depth, velocity, and cover parameters. Most site measurements of depth and velocity in the present study either had sufficient depths or sufficient velocities, but sites with the correct combination of both were rare. Such combinations may be present in larger streams.

Perhaps the most direct management application of our study was to simply aid identification of growth limitations and management potential. The best candidates for large trout management (MNDNR 2000) are streams with fast growth (MNDNR 1997). Incremental growth analysis showed that fast growth streams could be identified based on growth during the first year. Therefore, management biologists could evaluate growth potential from the length at age 1 during spring sampling. Mean length at age 1 can probably be estimated from a length-frequency histogram. Growth would be classified as slow when mean length at age 1 was < 125 mm and as fast when > 145 mm.

Alternatively, managers could identify streams based on water temperature and forage. Streams with maximum July water temperatures exceeding 19.0 °C would be good candidates for large trout management. Identification of candidate streams with colder temperatures would require further examination to determine forage composition and availability. Colder streams with an abundance of energy rich prey taxa, such as amphipods, mayflies, sculpin, and abundant smaller trout could be considered for large trout management. However, colder streams lacking these taxa would not be considered good candidates, but could be considered for reintroduction of these taxa to enhance growth rates of brown trout.

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## Appendix 1. *Brown trout bioenergetics model parameters*

To run the bioenergetics model requires estimates of 12-30 parameters that represent the major physiological processes of consumption, metabolism, egestion, and excretion (Hanson et al. 1997). The exact number of parameters depends on the target species and model functions selected to describe its energy balance. The revised Wisconsin bioenergetics model (Hanson et al. 1997) did not have estimates for consumption, metabolism, and waste parameters for brown trout; thus we reviewed other studies to obtain them. Primary information for development of model parameters comes from a series of extensive studies conducted by Elliott on the energetics of brown trout (Elliott 1975a, 1975b, 1976a, 1976b, 1994). Elliott's equations were developed for brown trout ranging from 5 to 300 g. Although application of these parameters to larger fish sizes may introduce some errors, extrapolation is a common practice in bioenergetics modeling because information on energetics of larger size groups is frequently lacking (Ney 1993; Hayes et al. 2000). Parameters not obtainable from Elliott's papers were obtained from information on other salmonids, principally rainbow trout *Oncorhynchus mykiss* (Rand et al. 1993; Hanson et al. 1997).

The Wisconsin bioenergetics model requires eight parameters to estimate consumption (Table 2). Consumption parameters CA and CB represent the intercept and slope, respectively, of an allometric mass dependence relationship (i. e., negative power relationship) between proportion of maximum consumption and fish weight conducted at an optimum temperature. Elliott (1975b) presented a multiple regression equation relating maximum weight of food consumed in a day (D) to fish weight and water temperature. His equation (equation 4 in Elliott 1975b) is:

$$D = A_D W^{b_1} e^{(b_3 T)} \quad (1)$$

where D = maximum weight of food consumed (mg/day), W = wet weight of brown trout (g), T = water temperature (°C), and A<sub>D</sub>, b<sub>1</sub>, and b<sub>3</sub> are constants from Elliott (1975b) that vary depending on water temperature. Elliott (1994) displays two figures that show the highest feeding rate at about 17.5 °C.

Also, Hayes et al. (2000) used 17.8 °C as the temperature for maximum consumption for their brown trout bioenergetics model. Therefore we used the appropriate constants, set T = 17.5 and estimated D for brown trout weights ranging from 5 to 450 g. After converting D to appropriate units (g/day), dividing by the original trout weights to get proportion of maximum consumption (g/g/day), and dividing by 0.25 (i.e., the approximate dry weight/wet weight ratio for amphipods used in Elliott's study) a negative power function was identified with slope = CB = -0.233 and intercept = CA = 0.2161.

The remaining six consumption parameters (Table 2) are defined by a temperature dependence function relating the proportional rate of food consumption to water temperature. The temperature dependence function is based on the Thornton and Lessem (1978) algorithm that essentially produces two sigmoid curves - one curve for the increasing proportion of the relationship and the second for the decreasing portion of the relationship (Hanson et al. 1997). Elliott (1975b) presented a statistical relationship between maximum rate of food consumption and water temperature and demonstrated that this relationship was independent of fish weight. We predicted maximum consumption rate for a range of water temperatures using the equation in Elliott (1975b) (i. e., his equation 9):

$$F = c e^{dT} \quad (2)$$

where F = rate of food consumed (mg/hr), T = water temperature (°C), and c and d are constants depending on water temperature. The bioenergetics model's consumption equation 3 requires defining F as some proportion of a maximum value. We defined maximum F (F<sub>max</sub>) as the value of F at 19.3 °C because this was the temperature at which Elliott's (1975b) equation predicted the highest feeding rate. Calculated F-values for each temperature were divided by F<sub>max</sub> and rescaled to appropriate units to get the proportional rate of food consumption for a range of temperatures. These values were used to identify appropriate model parameters (Table 2).

Respiration requires values for 11 parameters (Table 2). Parameters approximate relations between (1) standard metabolism (R<sub>s</sub>) and fish weight (parameters RA, RB) and

temperature (parameter RQ), (2) active metabolism ( $R_a$ ) and swimming speed (parameter RTO), (3) swimming speed and weight (parameters RK1, RK4, ACT), and (4) swimming speed and temperature (parameter BACT). Parameter RTL defines a cutoff temperature where the swimming speed/weight relationship changes. Parameter RTM is the maximum lethal water temperature if using equation 2 but is always set to 0 when using respiration equation 1 and swimming speed is not considered constant. Parameter SDA is the proportion of assimilated energy required to process food.

Information on brown trout standard metabolism was taken from Elliott's (1976b) studies on unfed brown trout. Elliott (1976b) assumed that experiments conducted on relatively inactive trout, deprived of food, closely approximated measurements of standard metabolism. We used his equation (9), and appropriate conversions, to estimate parameters RA, RB, and RQ. Estimation of remaining parameters required information on brown trout swimming speed and relations with weight, temperature, and respiration. However, these data are presently unavailable. Remaining respiration parameters were borrowed from published information on rainbow trout and other salmonids (Rand et al. 1993; Hanson et al. 1997). In most instances, these parameter estimates varied little among other salmonid species, possibly implying similarity among these coldwater taxa (Table 2).

Egestion/excretion parameters were taken from published reports of other salmonids (Beauchamp et al. 1989; Rand et al. 1993; Hanson et al. 1997) but are based primarily on information for brown trout provided by Elliott (1976a). Elliott's (1976a) experiments were conducted on amphipod-fed brown trout and represent one of the few studies that examined egestion/excretion with test fish fed wild foods as opposed to artificial pellets.

Energy density parameters were developed from equations to estimate energy density of brown trout from body weight in Hayes et al. (2000) for brown trout less than 810 g. Most brown trout in southeast Minnesota streams do not exceed this weight. We used a constant for K (i.e., condition factor) of

1.14 based on information in Carlander (1969) and predicted brown trout energy density for a range of body weights between 1 and 810 g. The resulting relationship was curvilinear and was well represented by two straight lines fitted by least-squares regression. The lines intersected at about 151 g and resulting model parameters were taken from these regressions.

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