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Laboratory Evaluation of Two Bioenergetics Models for Brown Trout

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Abstract. – Laboratory growth and food consumption data for two size classes of brown trout *Salmo trutta* that experienced three distinct feeding regimes at two temperatures were used to evaluate the abilities of two bioenergetics models to predict fish growth. Accuracy of cumulative consumption predictions was also tested for one of the models. Model errors for predicting relative growth rate of individual fish were regressed on observed mean daily consumption rate to assess whether consumption-dependent prediction error commonly observed in bioenergetics models for other fish species was exhibited by the two brown trout bioenergetics models. Both models yielded unbiased estimates of brown trout growth that were within 1-12% of observed values across the range of fish sizes, water temperatures, and ration levels tested. Bonferroni joint 95% confidence intervals for the slopes and intercepts of regressions of predicted final weight on observed final weight included a slope of 1 and a y-intercept of 0 for both models. No significant inter-model differences in percent error for predicting final weight of fish in feeding trials were observed. Predicted cumulative consumption values were within 8-15% of corresponding observed values. Neither model exhibited significant consumption-dependent error for predicting brown trout growth, in contrast to results of several previous laboratory evaluations of bioenergetics models for other fish species. Absence of consumption-dependent error in the two brown trout models may be due to incorporation of feeding rate-dependence of egestion and excretion in these models and that egestion and excretion parameters were not borrowed from other species. Results of this evaluation corroborate the utility of these bioenergetics models for predicting growth and consumption for brown trout under the range of fish sizes, water temperatures, and ration levels tested.

Bioenergetics models are commonly applied in fisheries management and research and have been used with increasing frequency in recent years to estimate fish growth or consumption (Hartman and Hayward 2007; Chipps and Wahl 2008). Evaluation of bioenergetics model predictions is an important step in model development and refinement and for highlighting model strengths and weaknesses that can guide subsequent model applications (Chipps and Wahl 2008). Ideally, reliability of bioenergetics model predictions should be assessed in both laboratory and field settings (Ney 1993; Chipps and Wahl 2008). Laboratory evaluations of fish bioenergetics models enable rigorous assessment of the adequacy of model parameters and equations because model input variables can be precisely measured under controlled conditions (Bajer et al. 2003; Madenjian et al. 2006). Indeed, several laboratory evaluations published during the past decade (e.g., Whitledge and Hayward 1997; Madenjian and O'Connor 1999; Chipps et al. 2000; Bajer et al. 2003; Whitledge et al. 2003; Madenjian et al. 2004; Madenjian et al. 2006; Whitledge et al. 2006) have provided substantial new insights into model strengths and weaknesses. However, reliability of growth and consumption predictions for bioenergetics models developed for several fish species have not yet been assessed, and those models that have been evaluated have rarely been tested over broad ranges of water temperature, fish size, and ration level (Chipps and Wahl 2008). Evaluation of bioenergetics model predictions over a wide range of conditions is important because models may be accurate only within particular ranges of water temperature, fish size, or ration level. For example, most bioenergetics models that have been evaluated in the laboratory using a variety of feeding rates have exhibited "consumption-dependent error" (Bajer et al. 2004a), which refers to the tendency of models to overestimate food consumption and underestimate growth rate for fish fed at low rations and to underestimate food consumption and overestimate growth rate for individuals that exhibit relatively high consumption and growth rates (Bajer et al. 2004a). Systematic consumption-dependent error has implications for reliability of model predictions in field applications (Bajer et al. 2004a), and has led to the development of regression-based correction procedures that can substantially improve model performance (Bajer et al. 2004b; Whitledge et al. 2006; Schoenebeck et al. 2008).

At least three bioenergetics models for brown trout *Salmo trutta* have been developed during the past decade (Elliott and Hurley 2000; Hayes et al. 2000; Dieterman et al. 2004). One of these models (hereafter referred to as the Hayes et al. model) is the bioenergetics component of a foraging and growth model for drift-feeding brown trout developed by Hayes et al. (2000). A second model is a Wisconsin bioenergetics model (Hanson et al. 1997) configured for brown trout (Dieterman et al. 2004) that is hereafter referred to as the Wisconsin model. The Hayes et al. model was designed to predict growth, whereas the Wisconsin model has the capacity to predict growth or food consumption. Both of these models were derived primarily from a series of laboratory experiments on invertebrate-fed brown trout (5-300 g wet weight) conducted by Elliott (1976a) and Elliott (1976b). Model parameters not obtainable from Elliott's papers were obtained from data for other salmonids, primarily rainbow trout *Oncorhynchus mykiss* (Stewart 1980; Rand et al. 1993). The Hayes et al. model has been demonstrated to produce reasonable estimates of size at age for drift-feeding brown trout in a New Zealand river (Hayes et al. 2000). However, neither the Hayes et al. nor Wisconsin models have been independently evaluated under controlled laboratory conditions. A third brown trout bioenergetics model developed by Elliott and Hurley (2000) was derived from data for piscivorous fish that were larger (>250 g wet weight) than those available for this model evaluation. The objectives of this study were to conduct a laboratory evaluation of growth predictions for the Hayes et al. and Wisconsin bioenergetics models for brown trout, to compare the relative performance of the two models for predicting growth, and to test the accuracy of the Wisconsin model's consumption predictions for brown trout at two temperatures across a range of fish sizes and ration levels. We also assessed the degree to which consumption-dependent error (Bajer et al. 2004a) was present in these models over the range of conditions tested.

Methods

Laboratory data sets

Growth and food consumption data were obtained from a laboratory study that evaluated the efficacy of several feeding schedules for improving growth and feed conversion ratio (including feeding regimes designed to elicit compensatory growth) in brown trout. Growth and consumption data for two size classes of fish fed using three distinctive feeding regimes at two temperatures were chosen so that the bioenergetics model evaluation would encompass a range of fish sizes, feeding levels, and temperatures given available data.

Two size classes of brown trout (small: age 8 months, mean weight 6.7 ± 0.4 g SE, mean length 9 cm; large: age 15 months, mean weight 112.1 ± 2.8 g SE, mean length 21 cm) were obtained from the Missouri Department of Conservation's Shepherd of the Hills Hatchery near Branson, Missouri and transported to the fisheries laboratory at the

University of Missouri-Columbia. Fish were acclimated to laboratory conditions for two weeks in 1100-L, circular tanks equipped with water recirculation, biofiltration, and temperature-control systems. Photoperiod was maintained at 14 h light:10 h dark throughout the laboratory acclimation period and subsequent feeding trials. Water temperature was held at 13 ± 1°C during acclimation and the first set of feeding trials described below. After two weeks in the laboratory, 16 small fish and 24 large fish were placed individually into perforated, open-top, plastic chambers (38 x 20 x 30 cm, 15 L for small fish; 28 x 30 x 41 cm, 30 L for large fish) that were partially submerged within elongated, 1000-L tanks equipped with biofiltration, water recirculation, and temperature control capacities, with eight chambers per tank. Test chamber tops protruded above tank water levels and were covered with removable plastic mesh to prevent fish from escaping their chambers, while also allowing feed to be readily delivered through the mesh apertures. Chamber covers were removed daily for short periods to enable removal of uneaten feed and feces. Fish were fed Silver Cup trout feed (45% protein, 18% fat) daily without restriction prior to initiation of feeding trials. To ensure that high water quality was maintained throughout acclimation and experimentation, 30% water replacement was conducted weekly for each of the 1000-L tanks. Temperature and dissolved oxygen levels were monitored daily in each tank (and periodically in the individual chambers), while nitrite and nitrate levels were determined weekly. Throughout the study, dissolved oxygen concentrations remained $\geq$9 mg/L and nitrite and nitrate levels did not exceed 0.25 and 30 mg/L, respectively, in any tank.

Feeding trials at 13 ± 1°C began in mid-July 2002 after allowing four weeks for fish to acclimate to individual housing in chambers and all fish were observed to consume feed regularly. Eight large fish (mean weight 113.7 ± 4.3 g SE) and eight small fish (mean weight 6.7 ± 0.6 g SE) were assigned to a control feeding regime in which fish were fed ad libitum twice daily with the same feed that was used prior to feeding trials. Eight fish from each size class (mean weights 6.7 ± 0.5 g SE and 111.6 ± 4.1 g SE for small and large fish, respectively) were assigned to a feeding regime that consisted of repeating cycles of two days of no feeding followed by multiple days of ad libitum feeding (hereafter referred to as the D2 feeding regime). Periods of twice daily ad libitum feeding for fish assigned to the D2 feeding regime were continued until hyperphagia (used to indicate active compensatory growth) ended. Hyperphagic periods were considered to end when mean daily consumption by large and small fish to which the D2 feeding regime was applied no longer exceeded that of control fish of the same size class for two consecutive days (one-tailed t-tests, $P>0.025$). When hyperphagia ceased, another two-day no-feed period began. Feeding trials were continued for 93 d for small fish and 97 d for large fish to which the control and D2 feeding regimes were applied, allowing fish in the small D2 and large D2 groups to complete 10 and 12 no-feed and reefed cycles, respectively. Growth and food consumption data for eight fish from the large size class (mean weight 111.1 ± 6.2 g SE) that were fed at a near-maintenance ration (0.35% body weight/d) daily for 14 d (hereafter referred to as the M14 group) were also used in bioenergetics model evaluations. Insufficient numbers of small fish were available to include a maintenance ration treatment for fish in the small size class. Each fish was weighed to the nearest 0.1 g at 10-14 d intervals during feeding trials. Uneaten feed pellets were removed at the end of each day and the number of feed pellets consumed daily was determined for each individually-held fish by subtracting the number of uneaten feed pellets from the total number of feed pellets provided on the same day. Daily consumption (g dry weight) was then calculated for each fish by multiplying the number of pellets consumed by mean weight of feed pellets.

A second set of feeding trials were conducted during January and February 2003 to provide additional growth and consumption data at a warmer temperature (15 ± 0.5°C) for brown trout bioenergetics model evaluations. Eight individuals from each of two size classes of fish (small: mean initial weight 35.5 ± 3.0 g SE and large: mean initial weight 192.4 ± 17.0 g SE) that had previously been used in the feeding trials described above were randomly selected from remaining fish for this second set of feeding trials (some fish from the first experiment were sacrificed for determination of proximate composition and caloric density). Fish used in the second set of feeding trials were fed daily to apparent satiation during the interval between the two feeding trials. All fish were held individually in chambers described previously and fed ad libitum twice daily for 28 d during the second feeding trial. Fish were weighed every 14 d; procedures for determining daily food consumption were identical to those described for the first feeding trial.

Bioenergetics modeling

Laboratory growth and consumption data were used to evaluate predictive abilities of the Hayes et al. and Wisconsin bioenergetics models for brown trout. Parameter values for the two models are reported in Hayes et al. (2000) and Dieterman et al. (2004). Model input variables included growth and daily consumption data for individual fish, water temperature, and energy densities of brown trout and pelleted feed.

Energy density for brown trout was set at the mean value (6,693 J/g wet weight ± 253 J/g wet weight SE) determined using bomb calorimetry for three fish from each size class sampled at the beginning and end of the first feeding trial. Brown trout energy densities were within the range of values reported for salmonids by Cummins and Wuycheck (1971). Energy density for pelleted feed was set at 21,128 J/g ± 47 J/g SE, the mean value for two samples of feed determined using bomb calorimetry; this value for feed energy density was assumed to be constant. For both models, fish were assumed to incur no additional activity costs above resting routine metabolism. Observations of brown trout suggested that fish held individually within the restricted volume of test chambers did not experience any significant activity costs due to swimming or social interactions. The assumption of constant, low activity cost has also been employed in previous laboratory studies that corroborated bioenergetics models for other fish species (Whitledge and Hayward 1997; Madenjian and O'Connor 1999; Whitledge et al. 2003; Madenjian et al. 2004; Madenjian et al. 2006; Whitledge et al. 2006).

Both brown trout bioenergetics models (Hayes et al. 2000; Dieterman et al. 2004) were used to generate growth predictions for individual fish. Simulations were run in the Statistical Analysis System (SAS) version 9.1 for the Hayes et al. model and in Bioenergetics 3.0 (Hanson et al. 1997) for the Wisconsin model. Daily growth (g/g) was predicted from observed daily temperature and consumption data, summed over consecutive days, and expressed as change in body weight (g) over the duration of feeding trials. The Wisconsin model was also used to generate cumulative consumption (g) predictions for individual fish over the duration of each feeding trial. Daily consumption (g) was predicted from daily changes in fish weight and water temperature;

daily changes in fish weights were estimated by linearly interpolating between initial and final observed weights. A single P-value (proportion of maximum consumption (C_{max}) consumed daily) was fitted to observed body weight change for each fish over the duration of each feeding trial to estimate the feeding rate required to achieve observed final weight. Daily consumption values were predicted using constant P-values for individual fish, summed over consecutive days, and expressed as cumulative consumption (g). The Hayes et al. model was designed solely to predict growth and was therefore not used to predict consumption.

Evaluation of model predictions

Model predictions of final weight (g) and cumulative consumption (g) for brown trout were compared with corresponding observed values for individual fish at the end of each feeding trial. Absolute values of percent error for predicting final weight and cumulative consumption for individual fish were calculated as

$$\text{Error (\%)} = (|\text{PRED} - \text{OBS}|)/\text{OBS} \cdot 100,$$

where PRED is the predicted value of fish final weight or cumulative consumption and OBS is the corresponding observed value. Absolute differences between predicted and observed values were used to evaluate model performance so that positive and negative errors in model predictions would not offset and yield false indications of good overall model performance. Mean values of absolute percent errors were calculated for each size class-feeding regime-temperature combination for each model. For each fish, differences in absolute values of percent error for predicting fish final weight generated by the Hayes et al. and Wisconsin models were also calculated (% error for Wisconsin model - % error for Hayes et al. model) and were used to calculate mean values for inter-model differences in percent error for fish of a given size class that experienced a particular feeding regime within each feeding trial. Paired t-tests (with α adjusted with Bonferroni's correction for multiple tests) were used to assess whether mean values of inter-model differences in percent error for predicting fish final weight for a given fish size, feeding regime, and water temperature were significantly different from zero ($P < 0.05$). Least-squares linear regressions were used to assess relationships between predicted and observed values for final weight (both models) and cumulative consumption (Wisconsin model only) for individual fish, with data from both size classes of fish, all feeding regimes, and both feeding trials included. Bonferroni joint confidence intervals were used to test the null hypothesis that regressions had a y-intercept of 0 and a slope of 1 (Neter et al. 1990).

Additionally, model errors for predicting relative growth rate (g/g/d) of individual fish over the duration of feeding trials were regressed on observed mean daily consumption rate (% body weight/d) to assess the degree to which consumption-dependent systematic error (Bajer et al. 2004a) was exhibited by the two brown trout bioenergetics models.

Results

Mean final weights predicted by the Hayes et al. and Wisconsin bioenergetics models for brown trout were within 1-12% of corresponding observed mean final weights of fish in feeding trials across the range of temperatures, feeding regimes, and fish sizes tested (Table 1). Both models performed best for fish in the large size class that were fed a near-maintenance ration daily (M14 group), but no patterns in model growth prediction errors related to fish size class or water temperature were evident among treatments that were applied to both size classes of brown trout. There were no significant inter-model differences in percent error for predicting final weight of fish within any of the fish size, feeding regime, and water temperature combinations used (paired t-tests; d.f. = 7; $P > 0.05$ for each test; Table 1). Significant linear relationships between predicted and observed final weights of brown trout were present for both the Hayes et al. model and the Wisconsin model ($r^2 = 0.99$; d.f. =1,55; $P < 0.0001$ for each model). Bonferroni joint 95% confidence intervals for the slopes and intercepts of regressions of predicted final weight on observed final weight incorporating data from all feeding regimes, temperatures, and fish sizes included a slope of 1 and a y-intercept of 0 for both models (Figure 1). Model errors for predicting relative growth rate (g/g/d) of individual fish over the duration of feeding trials were not significantly correlated with observed mean daily consumption rates (d.f. = 1,55; $P = 0.1$ for the Wisconsin model; d.f. = 1, 55; $P = 0.2$ for the Hayes et al. model).

Observed mean daily consumption rates ranged from 0.25 % body weight/d to 4.4 % body weight/d during feeding trials and were generally higher for fish in the small size class compared to fish from the larger size class for a given temperature and feeding regime (Figure 2). Cumulative consumption values predicted by the Wisconsin model were within 8.5-15.1% of corresponding observed values for brown trout across the range of temperatures, feeding regimes, and fish sizes tested (Table 2). Mean absolute percent errors for predicting cumulative consumption were slightly lower for fish in the small size class compared to their larger counterparts for a given water temperature and feeding regime. The relationship between cumulative consumption predicted by the Wisconsin model and observed cumulative consumption was highly significant ($r^2 = 0.98$; d.f. = 1,55; $P < 0.0001$; Figure 3). Bonferroni joint confidence intervals indicated that the y-intercept of the regression line (0.03) relating predicted and observed cumulative consumption was not significantly different from 0 ($P = 0.97$), but the slope of the regression line (0.93) was significantly less than 1 ($P < 0.001$; Figure 3).

Discussion

Overall, both the Hayes et al. and Wisconsin bioenergetics models yielded unbiased estimates of brown trout growth that were within 10% of observed values across the range of fish sizes, water temperatures, and ration levels tested, with the exception of the Hayes et al. model applied to small control fish at 13°C. Neither model was superior to the other for predicting brown trout growth. Both models used identical data sources for equations to describe components of the energy budget for brown trout (Elliott 1976a; Elliott 1976b; Stewart 1980; Rand et al. 1993), which likely accounts for the lack of significant inter-model differences in percent error for predicting growth of fish within any of the fish size, feeding regime, and water temperature combinations used in this evaluation. The Wisconsin model also yielded cumulative consumption estimates within 8.5-15.1% of corresponding observed values for brown trout, although model error for predicting consumption increased with higher feeding rates. Percent errors for predicting growth and consumption by the Hayes et al. and Wisconsin models for brown trout in this evaluation were on the low end of the range of percent errors for predicting growth and consumption reported in published laboratory evaluations of bioenergetics models for other fish species (Whitledge and Hayward 1997; Madenjian and O’Connor 1999; Chipps et al. 2000; Bajer et al. 2003; Paakkonen et al. 2003; Whitledge et al. 2003; Bajer et al.

2004b; Chipps and Wahl 2004; Madenjian et al. 2004; Madenjian et al. 2006; Whitledge et al. 2006; Madenjian et al. in press). Thus, the Hayes et al. and Wisconsin bioenergetics models for brown trout appear to be two of the most reliable models for predicting fish growth and consumption among those models that have been independently evaluated in the laboratory, at least under the range of fish sizes, ration levels, and near-optimum temperatures included in this study. The overall reliability of the Hayes et al. and Wisconsin bioenergetics model predictions of growth and consumption may be due to the fact that these models were parameterized primarily using data describing functional relationships between fish size and water temperature and energy budget components (consumption, respiration, egestion, and excretion) that were obtained directly from laboratory experiments on brown trout (Elliott 1976a; Elliott 1976b) rather than being borrowed from other species.

Neither the Hayes et al. nor the Wisconsin bioenergetics models exhibited significant consumption-dependent error rates for predicting growth of brown trout, in contrast to results of several previous laboratory evaluations of bioenergetics models for other fish species (Bajer et al. 2004a; Chipps and Wahl 2008). The apparent absence of consumption-dependent error in the two brown trout bioenergetics models suggests that parameter values and functions for consumption-influenced components of the energy budget (egestion (F), excretion (U), and specific dynamic action (SDA)) were adequately characterizing relationships between consumption rate and F, U, and SDA over the range of ration levels and feeding regimes included in this evaluation. The lack of significant correlations between observed consumption rate and growth prediction errors for the two brown trout models tested may be due to the fact that F and U are modeled as functions of ration size, body weight, and temperature rather than fixed proportions of consumed energy and that F and U parameters for both brown trout models were obtained from data on conspecifics (Elliott 1976a; Elliott 1976b) rather than being borrowed from other species. Borrowing of parameter values, particularly those related to F and U, is common among bioenergetics models (Ney 1993; Hanson et al. 1997). Results of this study suggest that using F and U parameters obtained from the fish species being modeled rather than borrowing F and U parameters from other species may result in lower consumption-dependent error in model predictions of growth and food consumption.

The results of this evaluation corroborate the utility of the Hayes et al. and Wisconsin bioenergetics models for predicting growth (both models) and consumption (Wisconsin model only) for brown trout under the range of fish sizes, water temperatures, and ration levels tested. However, this evaluation was limited to two temperatures near the growth optimum for brown trout and did not include fish larger than 285 g wet weight. Consideration of the range of conditions under which bioenergetics models have been corroborated is important for assurance of reliability of growth or consumption predictions in field applications of bioenergetics models (Chipps and Wahl 2008). Hence, we recommend application of the Hayes et al. and Wisconsin bioenergetics models for brown trout to fish < 300 g wet weight and suggest that additional evaluation be conducted prior to application of these models to larger fish. Further assessment of the accuracy of model growth and consumption predictions at both higher and lower temperatures is also recommended before either of these two bioenergetics models is applied to brown trout at temperatures beyond the range of those used in this study. Independent evaluation of the bioenergetics model developed for larger, piscivorous brown trout (Elliott and Hurley 2000) is also warranted. Additional evaluation of brown trout bioenergetics models using the approach described in Madenjian et al. (2000) would also be valuable for assessing the reliability of model predictions under field conditions.

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Table 1. Mean (SE) observed final weights (g) for two size classes of brown trout in control (fed ad libitum daily), D2 and M14 treatment groups at two temperatures and mean (SE) predicted final weights (g) for fish in the same groups generated by the Hayes et al. bioenergetics model (Hayes et al. 2000) and the Wisconsin bioenergetics model (Dieterman et al. 2004). Mean absolute values of percent errors (SE) for predicting final weights of fish in each group are reported for both models. n=8 fish for each treatment.

Temperature 13°C

		Hayes et al. model		Wisconsin model	
Group	Observed final weight	Predicted weight	% error	Predicted weight	% error
Large control	170.0 (11.5)	170.4 (11.3)	3.0 (0.8)	179.4 (10.9)	6.4 (1.3)
Large D2	175.4 (11.1)	167.6 (9.0)	4.7 (1.3)	179.8 (9.5)	4.9 (1.4)
Large M14	114.6 (6.3)	113.1 (5.9)	1.5 (0.3)	114.7 (6.0)	0.9 (0.3)
Small control	21.5 (2.9)	19.8 (2.1)	11.8 (1.8)	22.3 (2.2)	9.2 (3.9)
Small D2	27.0 (2.4)	26.8 (1.9)	6.2 (2.8)	26.0 (1.8)	7.2 (2.4)

Temperature 15°C

		Hayes et al. model		Wisconsin model	
Group	Observed final weight	Predicted weight	% error	Predicted weight	% error
Large control	212.5 (21.9)	211.2 (19.8)	5.9 (1.1)	214.9 (19.7)	6.3 (0.9)
Small control	46.2 (4.9)	47.7 (4.4)	5.2 (1.4)	48.2 (4.4)	6.1 (1.6)

Table 2. Mean observed cumulative consumption (g) for two size classes of brown trout in control (fed ad libitum daily), D2 and M14 treatment groups at two temperatures, mean (SE) cumulative consumption (g) for fish in the same groups predicted by the Wisconsin bioenergetics model (Dieterman et al. 2004), and mean absolute value of percent error (SE) for predicting cumulative consumption by fish in each group.

Temperature 13°C

Group	Observed cumulative consumption	Predicted cumulative consumption	% error
Large control	70.3 (6.7)	63.0 (7.2)	12.0 (2.4)
Large D2	71.9 (4.8)	68.5 (6.1)	9.1 (2.6)
Large M14	5.4 (0.1)	5.4 (0.3)	12.2 (3.1)
Small control	15.0 (1.5)	14.4 (2.1)	9.1 (3.4)
Small D2	17.9 (1.5)	18.7 (2.0)	8.5 (2.9)

Temperature 15°C

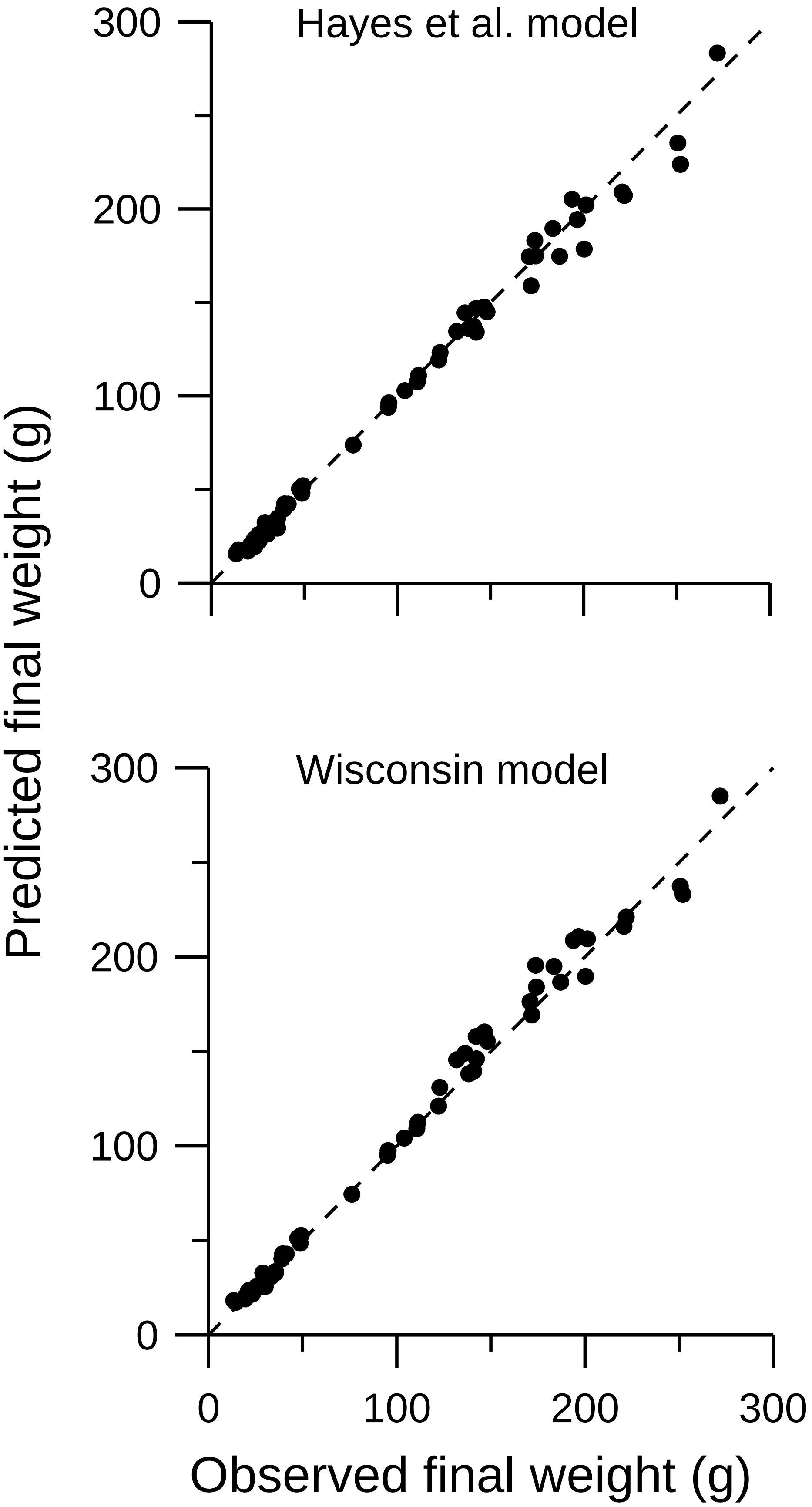
Group	Observed cumulative consumption	Predicted cumulative consumption	% error
Large control	26.6 (4.8)	24.8 (4.5)	15.1 (4.1)
Small control	12.5 (1.3)	10.9 (1.8)	12.8 (3.7)

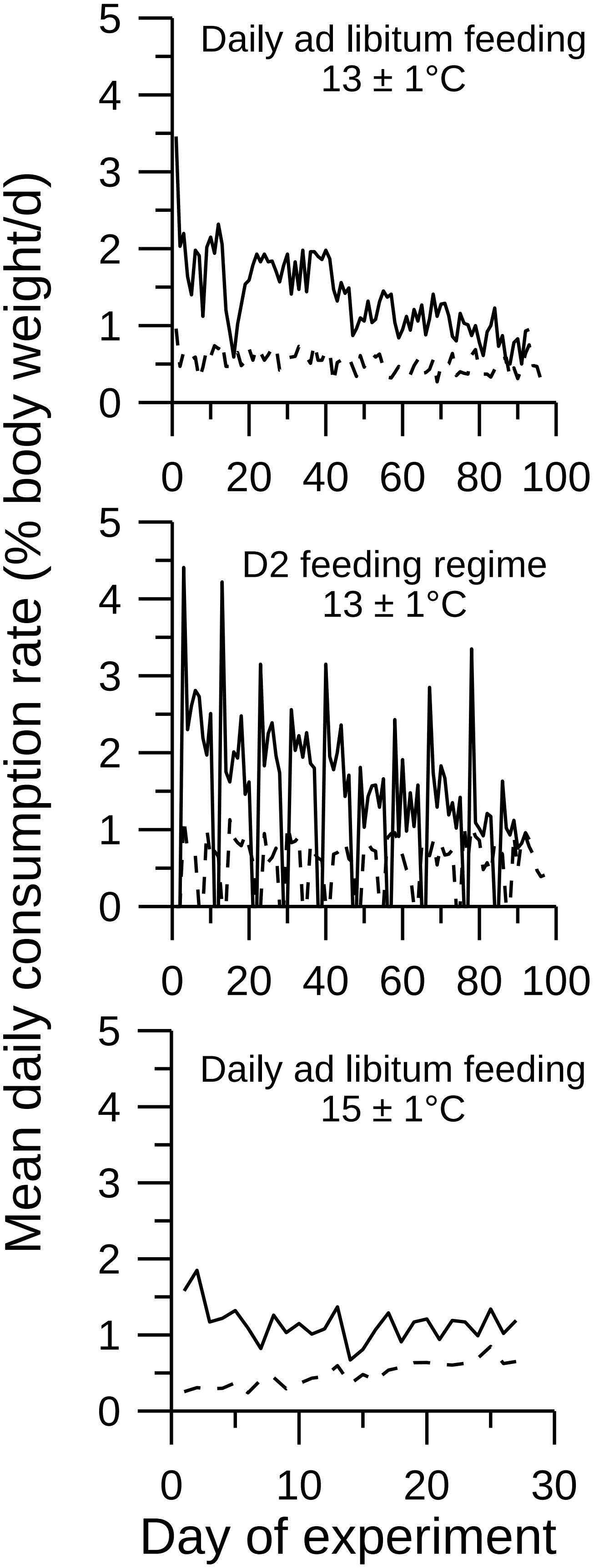
Figure Captions

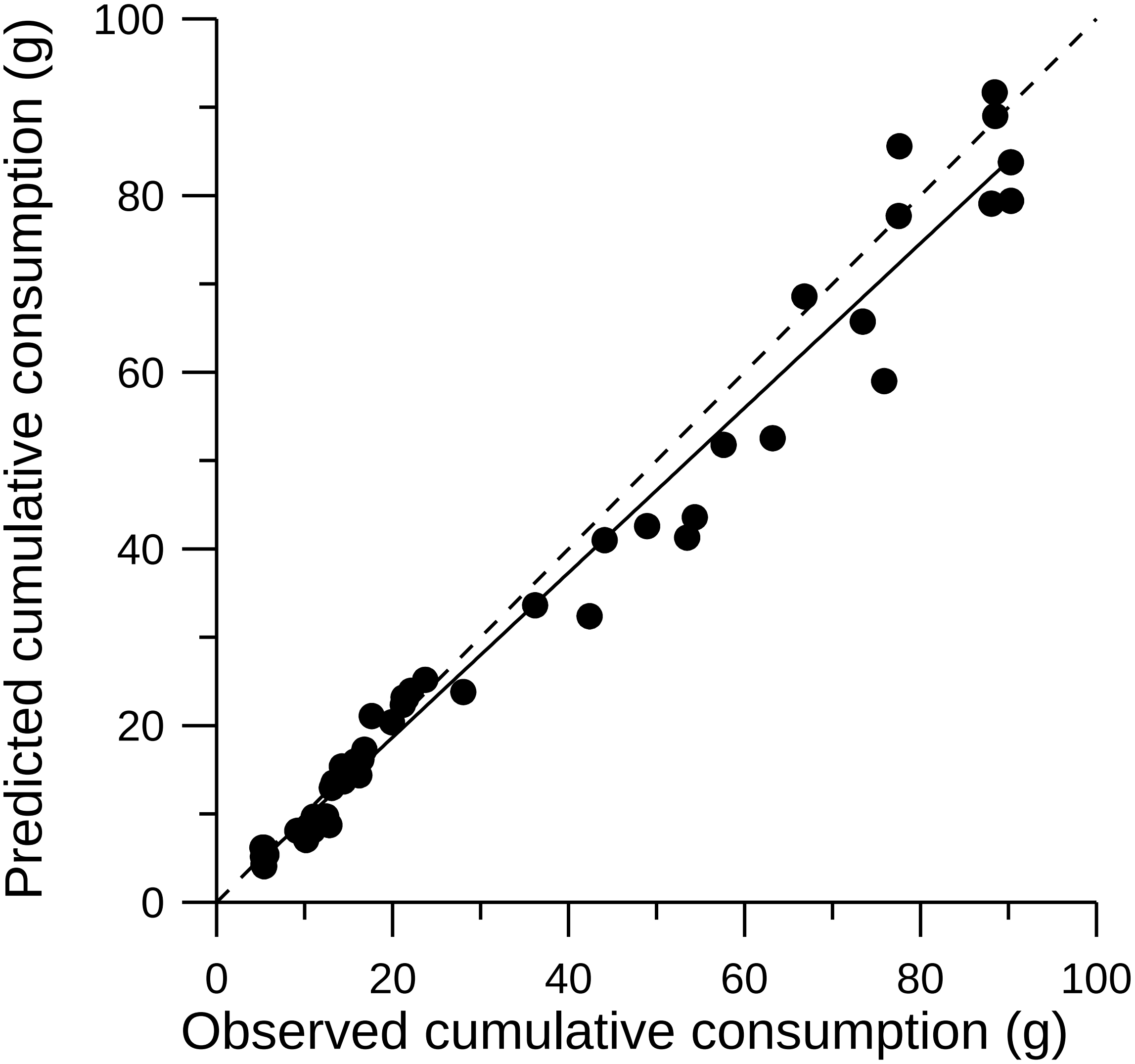
Figure 1. Predicted final weights (g) for individual brown trout (n=56) from all experimental treatments as a function of observed final weight (g) for the Hayes et al. bioenergetics model (Hayes et al. 2000) and the Wisconsin bioenergetics model (Dieterman et al. 2004). Dashed lines in each panel represent 1:1 correspondence between predicted and observed values.

Figure 2. Mean observed daily consumption rates (% body weight/d) for small (solid line) and large (dashed line) size classes of brown trout fed ad libitum daily (control fish) at 13 ± 1°C, small (solid line) and large (dashed line) size classes of fish fed using the D2 feeding regime at 13 ± 1°C, and small (solid line) and large (dashed line) size classes of fish fed ad libitum daily at 15 ± 1°C.

Figure 3. Cumulative consumption (g) predicted by the Wisconsin bioenergetics model (Dieterman et al. 2004) for individual brown trout (n=56) from all experimental treatments as a function of observed cumulative consumption (g). The solid line represents the regression line fit to data and the dashed line represents the line of 1:1 correspondence between predicted and observed values.


Hayes et al. model
Wisconsin model
300
200
100
0
300
200
100
0
0
100
200
300
Predicted final weight (g)
Observed final weight (g)


Mean daily consumption rate (% body weight/d)
Daily ad libitum feeding
13 ± 1°C
D2 feeding regime
13 ± 1°C
Daily ad libitum feeding
15 ± 1°C
0
1
2
3
4
5
0
20
40
60
80
100
0
10
20
30
Day of experiment


Predicted cumulative consumption (g)
Observed cumulative consumption (g)
0
20
40
60
80
100
0
20
40
60
80
100