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## Individual Variation in Bioenergetic Rates of Young-of-Year Rainbow Trout

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**Abstract.**—Studies collecting data on bioenergetic rates in fish typically measure the rates of a large number of individuals once and then fit parameters to those data sets. Such data commonly have large amounts of variation around the mean, which is left unexplained because the study aims to address population-level or ecosystem-level questions. We addressed the question of whether individual fish have detectably different rates of maximum consumption and respiration rates by repeatedly measuring those rates in individually identified young-of-year (age-0) rainbow trout *Oncorhynchus mykiss* over a range of temperatures. In experiment 1 we measured the respiration rates of two size-classes of age-0 rainbow trout five times at five different temperatures (9–19°C). In experiment 2 we measured the respiration and maximum feed consumption rates of one size-class of rainbow trout five times at four different temperatures (7–19°C). We also use these data to develop a new parameter set for a Wisconsin bioenergetics model of maximum consumption and respiration rates for age-0 rainbow trout. The results show that individual differences have a significant effect on their respiration and maximum feed consumption rates. The new bioenergetics parameter set differs considerably from the parameter sets developed for adult rainbow trout. The new bioenergetics model may prove useful for studies examining the growth and feed consumption of age-0 rainbow trout. The finding of significant differences between individuals in measured rates of respiration and maximum consumption may be important in individual-based models (IBMs) of fish populations. Specifically, IBMs have not included individual-level differences in bioenergetic rates, but such differences may have an important effect on their predictions of fish growth, production, and population number.

Bioenergetic models of fish consumption and respiration rates have served the science of fisheries and fish biology well since their inception in the late 1970s (Kitchell et al. 1977; Thornton and Lessem 1978). The papers in this symposium and the one held in 1992 demonstrate the importance of these models to both basic and applied fisheries science (Brandt and Hartman 1993). Bioenergetic models have played important roles in a variety of ecological and fisheries analyses, including energy transfer among trophic levels (Carpenter 1988), fish stocking regimes (Rand et al. 1995), habitat suitability for specific species (Roy et al. 2004), and environmental effects on fish populations (Brandt et al. 2002).

The maturation of bioenergetic models of fish growth has played a critical role in the development of individual-based models (IBMs) of fish populations (for reviews, see DeAngelis et al. 1990; Tyler and Rose 1994; Giske et al. 1998; Werner et al. 2001; Salvanes 2001). Fish population IBMs have extensively de-

scribed how events may affect individuals differently. Examples of this include how population or cohort survivorship may be affected by small differences in size (DeAngelis et al. 1979; Rose and Cowan 1993), the timing of migrations (Adams and DeAngelis 1987), and environmental changes that have seemingly small effects on individual growth (Cowan et al. 1993). One of the consistent themes that arises from various IBM studies is that seemingly small differences in individual fish can have an effect on overall population dynamics—that what happens to the special few individuals that survive to reproduce disproportionately affects the population (DeAngelis and Gross 1992).

Studies collecting data and developing bioenergetic models of fish growth have shown that endogenous and exogenous factors can significantly affect these rates. Bioenergetic rates differ by species and size-class (reviewed in Hanson et al. 1997). Environmental factors such as temperature (Hanson et al. 1997), dissolved oxygen concentration (Zhou et al. 2001), and salinity (Wuenschel et al. 2005) also affect bioenergetic rates.

Data collected on the key bioenergetic rates of respiration and maximum consumption typically exhibit large amounts of variation around mean values

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(Rao 1968; Hartman and Brandt 1995; Myrick and Cech 1996). Often this variation in the measured rates is considered experimental error because experimenters must handle individual fish considerably to put them into various apparatuses to collect the data. Also, the aim of most studies examining fish bioenergetics is to look for large trends in important rates that determine fish growth. Therefore, these studies have considered variation from the mean to be statistical noise. Because IBMs of fish populations consistently find that individual differences affect population dynamics and because physiological differences in individuals often are not well depicted in these models (Chambers 1993), the question of whether variation in bioenergetic rates results from detectable individual differences deserves attention.

In this paper we examine the question of whether variation from the mean rates of respiration and maximum consumption is a consistent and measurable feature of the individual fish. The experiments in this study consisted of repeatedly measuring respiration and maximum consumption rates in young-of-year (age-0) rainbow trout *Oncorhynchus mykiss* as they grew and at different water temperatures. In addition, previous studies have developed bioenergetic models for adult rainbow trout (Rand et al. 1993; Railsback and Rose 1999), but not for age-0 rainbow trout. We used the data collected here to develop a parameter set specific to age-0 rainbow trout for the respiration and maximum consumption portion of the Wisconsin bioenergetics model.

### Methods

To determine whether individual fish consistently differ in their respiration and maximum consumption rates, we conducted two laboratory experiments. The first experiment measured respiration in two age-classes (i.e., large and small size-classes) of rainbow trout over five temperatures. The second experiment measured respiration and maximum consumption in one size-class (medium) of rainbow trout over four temperatures. In both experiments we identified all individual fish with either numbered streamer tags (medium and large fish) or fin clips (small fish only) and measured their weights at the conclusion of each trial.

*Fish source, diet, and holding tanks.*—We obtained age-0 rainbow trout from the Redwing Trout Hatchery in Montague, Massachusetts. The laboratory holding facility consisted of four 135-L holding tanks in a recirculating system. An overflow pipe in all four tanks allowed for water pumped into each tank to continuously flow into a 750-L head tank. The head tank regulated water temperature, filtered the water, and

pumped it back to the four tanks. The tank was equipped with two chillers, a heater, four filters (two fluidized bed filters and two cartridge filters), and two pumps. The fish were received from the hatchery 4 weeks before the start of each experiment. During the preexperiment period, fish were fed a commercial diet (dense culture crumble; Aquatic Ecosystems FA2) ad libitum and held at 14°C (SD = 2). The diet is the same food as that used in the experiments and similar to that used in the hatchery from which the fish came.

*Experiment 1: Respiration in two size-classes.*—In experiment 1 (April 2004 to June 2004), we collected respiration data from two groups of rainbow trout. The group of small rainbow trout consisted of 15 individuals (starting mean weight = 2.05 g, SD = 0.36) that were spawned in the spring of 2004. We divided one of the four holding tanks into three equal sections and placed five small fish in each section; the fish in each section were uniquely fin-clipped for identification. The group of large fish included 20 individuals (starting mean weight = 61.19 g, SD = 12.048) that were spawned in the spring of 2003. The 20 large fish were divided among the remaining three tanks and tagged with uniquely numbered streamer tags (Hallprint Corp.) for identification. Before being tagged, they were anesthetized in a bath containing tricane methanesulfonate (MS-222) at 0.04 g/L of water (Schreck and Moyle 1990).

The respiration rate experiments were performed on each fish multiple times over a range of different temperatures. The fish were allowed to acclimate to the water temperature for at least 36 h before each trial and fasted for at least 60 h before a trial. Respiration rates were measured as the rate of oxygen consumed by an individual inside a sealed chamber over a timed period. The dissolved oxygen (DO) concentration was measured at the beginning and end of each timed period using a YSI 550 DO probe.

The respirometers used in the study were plastic jars with airtight covers that were modified with a bulkhead fitting to provide a quick entry point for the DO probe. During experiments the bulkhead was sealed with multiple layers of parafilm. The chambers were of three different sizes (0.56, 2.19, and 3.91 L); the size of the fish determined the size of the chamber used. Tests of this system showed that without fish inside the chamber there was no change in the DO readings taken hours apart.

For each measurement we placed one fish inside a respirometer that was then submersed in the head tank and sealed underwater. Timing began when the cover was secure. The period over which oxygen consumption was measured ranged from 30 to 150 min, depending on size of the individuals in the chambers,

water temperature, and the size of the respirometer used. The starting DO was always 100%, as this was the concentration in the head tank. The sealed respirometer was then placed in one of the four holding tanks to maintain the chamber temperature throughout the timed period. Before the experiments, the fish were repeatedly handled in an identical manner until they showed no outward signs of stress (unusual swimming pattern or increased gill movement). Most fish showed no signs of stress on the first or second introduction to the respirometers. Fish that did not move easily to the respirometer after five attempts were not included in the study. After the timed period, the respirometer was removed from the holding tank, the parafilm over the bulkhead was punctured, and the DO probe was immediately inserted into the respirometer, expunging the water in immediate contact with the parafilm. For statistical analysis and to account for the effect of temperature on the saturation concentration of oxygen, DO measurements were collected as the percent DO remaining and were converted to milligrams of oxygen consumed per gram of fish weight per day. To calibrate the new respiration model we converted oxygen consumption to grams ( $\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ ).

The respiration experiments were performed on each individual five times at five temperatures: 9, 11, 13, 17, and 19°C. We randomized the sequence of temperature treatments and took only one set of respiration measurements in a day. We obtained a full set of five respiration measurements at each temperature for 9 small and 18 large fish; 6 small fish and 2 large fish were lost owing to various events during the study, and their data were excluded from the analyses.

*Experiment 2: respiration and maximum consumption in one size-class.*—In experiment 2 (November 2004 to February 2005), we collected both respiration and maximum feed consumption rates for one size-class of 28 rainbow trout (mean starting weight = 14.45 g, SD = 3.016) that were spawned in the spring of 2004. Each fish was individually identified with a numbered streamer tag using the same procedure as described in experiment 1. We divided the fish evenly among the four holding tanks. Respiration measurements were conducted in a method identical to that described in experiment 1.

The rainbow trout in the consumption experiment were acclimated to the water temperature and fasted the same amount of time as the fish in the respiration protocol. Maximum consumption was measured by the amount of food an individual consumed in two 1-h periods 16 h apart. Each fish was placed inside a consumption container, a 5 L bucket with a mesh cover, which was held in one of the four holding tanks to maintain the container's water temperature. An

amount of feed (dense culture crumble; Aquatic Ecosystems FA2), that exceeded that the fish would eat was weighed and distributed into each container at the beginning of the trial. At the end of the hour, the remaining food was filtered (feces were discarded). The food was placed in a drying oven at 63.5°C for 48 h. The dried filters were weighed to determine the amount of food not consumed, which was subtracted from the amount put into the feeding chamber at the start of the timed period to estimate the amount of food each individual consumed in that hour. For each fish the amount of food consumed in the two 1-h periods was combined to obtain the grams of food consumed per gram of fish per day.

Respiration and maximum feed consumption measurements were collected five times for each individual at four temperatures: 7, 11, 15, and 19°C. As with the previous experiment, we randomized the sequence of temperature treatments, and only one measurement was taken in a day. We obtained a full set of measurements for 26 fish; 2 fish were lost owing to various events, and their data were excluded from the analyses.

*Statistical analysis.*—To determine whether individuals showed consistent differences in their respiration and maximum consumption rates, we analyzed the data from experiments 1 and 2 with a mixed-model analysis of covariance (ANCOVA) using the SPSS statistical package. In this analysis, temperature is treated as a fixed factor, individual as a random factor, and weight as a covariate. We treated weight as a covariate because it is intimately linked to the individual and because it changes throughout the course of the experiment. We analyzed the three groups of rainbow trout (small and large from experiment 1 and medium from experiment 2) separately for the respiration measurements. To assess the amount of variability explained by the factors in the ANCOVA, we computed the correlation of the model to the data ( $R^2$ ) as  $1.0 - (\text{sum of squared errors} / \text{total sum of squares})$ .

We also fit a new set of parameters for the Wisconsin bioenergetics respiration and maximum feed consumption models to the data that we collected in these experiments. For this we conducted a simple grid search, systematically adjusting the values of the five respiration parameters and the eight maximum consumption parameters (see below) to obtain the set that best fit our respiration and maximum feed consumption data (see Hanson et al. 1997 for definitions of the parameters and equations). We ranked the fit of the predictions to our data based on correlation coefficients ( $r^2$ ). After selecting the set with the highest correlation, we adjusted the range and resolution of the grid search and repeated. We began with values published by Railsback and Rose (1999)

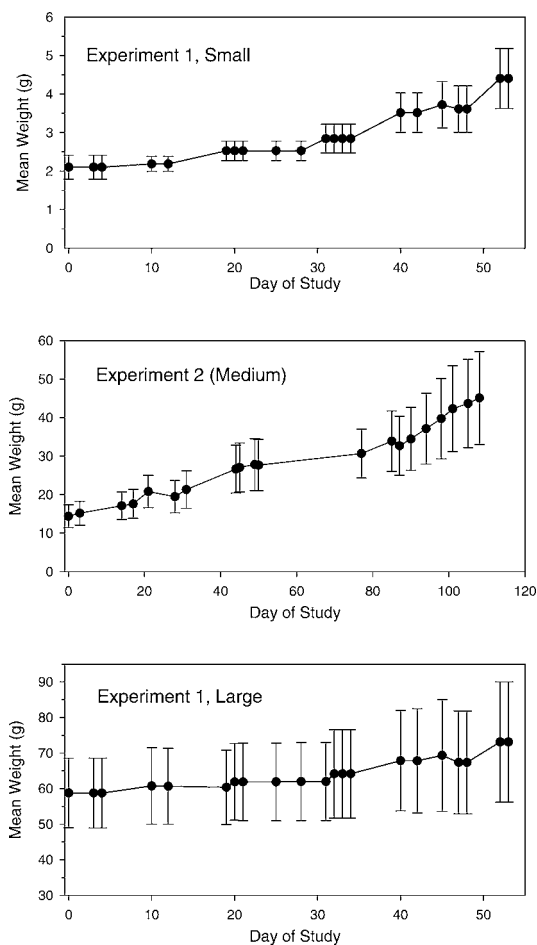


FIGURE 1.—Mean  $\pm$  SD weights of small, medium, and large age-0 rainbow trout during two experiments measuring their respiration rates.

and searched values over a range that was 0.5 and 2.0 times the initial values. We refined the range and resolution of the search until all parameter values changed by less than 0.1% and the correlation between model predictions and our data did not change.

The experiments conducted by Hokanson et al. (1977) and our own experience holding rainbow trout in the laboratory showed that temperatures above about 24°C result in increased mortality for rainbow trout. Therefore, we limited the parameter optimization algorithm so that it would not produce viable maximum consumption and respiration rates at temperatures above 24°C.

### Results

The rainbow trout were weighed regularly throughout the course of the study on the same days as the

TABLE 1.—Analysis of covariance of respiration rates for small rainbow trout (age 0) in experiment 1. Because the analysis mixes fixed and random factors with a covariate, each source of variation has its own error term and degrees of freedom are not always integers.

Source	df	Mean square error	F	P
Intercept	1.0	$9.29 \times 10^{-4}$	204.54	0.000
Intercept error	134.2	$4.54 \times 10^{-6}$		
Weight (covariate)	1.0	$8.65 \times 10^{-8}$	0.02	0.880
Weight error	179	$3.90 \times 10^{-6}$		
Temperature (fixed factor)	4.0	$3.56 \times 10^{-4}$	67.75	0.000
Temperature error	38.5	$5.26 \times 10^{-6}$		
Individual (random factor)	8.0	$2.42 \times 10^{-5}$	4.47	0.001
Individual error	32.8	$5.41 \times 10^{-6}$		
Temperature $\times$ individual	32.0	$5.44 \times 10^{-6}$	1.40	0.091
Temperature $\times$ individual error	179.0	$3.90 \times 10^{-6}$		

respiration trials. The weights of rainbow trout generally increased over time in both experiments 1 and 2 (Figure 1). In experiment 1 the small fish gained an average 2.3 g and the large fish 14.4 g. The duration of experiment 2 was considerably longer than that for experiment 1 because the data collected included both respiration and maximum feed consumption measurements; these fish gained an average 30.7 g during the experiment.

### Analysis of Individual Differences

The analysis of respiration rates showed significant effects of individual differences for the small (Table 1), medium (Table 2) and large (Table 3) age-0 rainbow trout. For the small and medium fish, the effect of individual differences on respiration was significant ( $P \leq 0.001$ ). The analysis revealed that water temperature also had a statistically significant effect on respiration rates for all groups, which is consistent with previous

TABLE 2.—Analysis of covariance of respiration rates for medium rainbow trout (age 0) in experiment 2.

Source	df	Mean square error	F	P
Intercept	1.0	$7.87 \times 10^{-4}$	602.12	0.000
Intercept error	83.4	$1.31 \times 10^{-6}$		
Weight (covariate)	1.0	$6.80 \times 10^{-6}$	10.04	0.002
Weight error	415.0	$6.77 \times 10^{-7}$		
Temperature (fixed factor)	3.0	$3.95 \times 10^{-4}$	627.64	0.000
Temperature error	79.0	$6.29 \times 10^{-7}$		
Individual (random factor)	25.0	$6.84 \times 10^{-6}$	10.88	0.000
Individual error	77.0	$6.28 \times 10^{-7}$		
Temperature $\times$ individual	75.0	$6.28 \times 10^{-7}$	0.93	0.648
Temperature $\times$ individual error	415.0	$6.77 \times 10^{-7}$		

TABLE 3.—Analysis of covariance of respiration rates for large rainbow trout (age 0) in experiment 1.

Source	df	Mean square error	F	P
Intercept	1.0	$6.40 \times 10^{-6}$	2.92	0.088
Intercept error	345.6	$2.19 \times 10^{-6}$		
Weight (covariate)	1.0	$3.14 \times 10^{-7}$	0.14	0.705
Weight error	339.0	$2.18 \times 10^{-6}$		
Temperature (fixed factor)	4.0	$1.06 \times 10^{-5}$	3.34	0.015
Temperature error	68.3	$3.18 \times 10^{-6}$		
Individual (random factor)	16.0	$5.47 \times 10^{-6}$	1.82	0.048
Individual error	68.3	$3.01 \times 10^{-6}$		
Temperature $\times$ individual	64.0	$3.23 \times 10^{-6}$	1.53	0.072
Temperature $\times$ individual error	339.0	$2.11 \times 10^{-6}$		

findings (Jobling 1994; Hanson et al. 1997). The interaction of temperature and individual had no significant effect on respiration. In experiment 1, the model for small fish (Table 1) explained a high fraction of the variation in the data ( $R^2 = 0.796$ ). In experiment 2 (Table 2) the correlation between the model and the data was even higher ( $R^2 = 0.887$ ). In experiment 1, large fish (Table 3) the model explained a much lower fraction of the variation in the data ( $R^2 = 0.324$ ).

Analysis of the maximum feed consumption rates from experiment 2 showed that the effect of individual differences was significant ( $P \leq 0.001$ ; Table 4), similar to the analysis of respiration rates. As expected, water temperature also had a significant effect on maximum consumption. In the ANCOVA of maximum consumption rates, the model explained an extremely high fraction of the variation in the data ( $R^2 = 0.909$ ).

#### New Bioenergetics Model Parameters

The respiration and maximum consumption data allowed us to develop a parameter set for the maximum consumption and respiration rates of the Wisconsin

TABLE 4.—Analysis of covariance of maximum feed consumption rates of rainbow trout (age 0) in experiment 2.

Source	df	Mean square error	F	P
Intercept	1.0	3.79E-01	2043.24	0.000
Intercept error	97.2	$1.86 \times 10^{-4}$		
Weight (covariate)	1.0	$2.02 \times 10^{-2}$	190.74	0.000
Weight error	415.0	$1.06 \times 10^{-4}$		
Temperature (fixed)	3.0	$3.26 \times 10^{-3}$	35.18	0.000
Temperature error	79.3	$9.26 \times 10^{-5}$		
Individual (random)	25.0	$8.33 \times 10^{-4}$	9.01	0.000
Individual error	77.0	$9.25 \times 10^{-5}$		
Temperature $\times$ individual	75.0	$9.23 \times 10^{-5}$	0.87	0.766
Temperature $\times$ individual error	415.0	$1.06 \times 10^{-4}$		

TABLE 5.—New parameters for the maximum consumption and respiration rate equations of the Wisconsin fish bioenergetics model for age-0 rainbow trout. The parameter definitions adapted from Hanson et al. (1997).

Parameter	Value	Definition
<b>Consumption</b>		
CA	0.1775	Intercept of the mass dependence function for consumption
CB	-0.297	Exponent of the mass dependence function for consumption
CQ	0.06	Temperature at which consumption is the lower fraction of the maximum (CK1)
CTO	14.5	Temperature at which consumption is 98% of the maximum on the increasing portion of the temperature dependence curve
CTM	20.5	Temperature at which consumption is 98% of the maximum on the decreasing portion of the temperature dependence curve
CTL	22.0	Temperature at which consumption is the upper fraction of the maximum (CK4)
CK1	0.397	Consumption fraction at water temperature CQ
CK4	0.655	Consumption fraction at water temperature CTL
<b>Respiration</b>		
RA	0.01166	Intercept of the mass dependence function for respiration
RB	-0.0558	Exponent of the mass dependence function for respiration
RQ	2.792	Approximation of the slope of the respiration function at low water temperatures
RTO	18.0	Optimal temperature for respiration
RTM	25.5	Maximum (lethal) temperature for respiration

bioenergetics model (Hanson et al. 1997) for age-0 rainbow trout (Table 5). The parameter set that our optimization routines created gives predictions of respiration and maximum feed consumption rates that differ notably from those created from the parameters developed for adult rainbow trout by Rand et al. (1993) and by Railsback and Rose (1999). The respiration rates predicted by the two adult rainbow trout models typically fall below those that we collected. The relationship between respiration rate and temperature shows adult predictions that are lower than the measured age-0 respiration rates and an optimal temperature that exceeds the temperature supported by the data (Figure 2). The relationship between respiration rate and fish weight predicted by the adult models differs from the same relationship described by new age-0 model or the data, but this difference is not terribly great (Figure 3).

The maximum feed consumption rates predicted by the two adult models differ notably from the rates measured for age-0 rainbow trout. The relationship between temperature and maximum consumption rates predicted by the two adult models predicts rates that are much higher than those we observed (Figure 4). The same is true for the relationship between weight and maximum feed consumption (Figure 5). In addition,

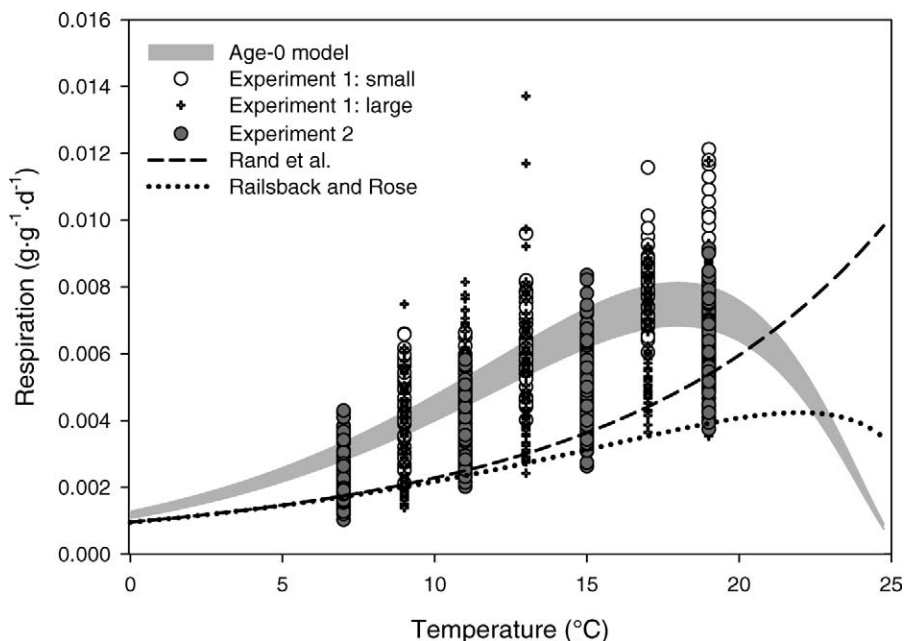


FIGURE 2.—Data and model predictions of the relationship between temperature and the respiration rate of age-0 rainbow trout. The data are shown as individual points. The shaded region shows the predictions from the new age-0 model over the range of weights determined by the mean weights of the small and large fish in experiment 1. The predictions from the models of Rand et al. (1993) and Railsback and Rose (1999) use the mean weight of all fish.

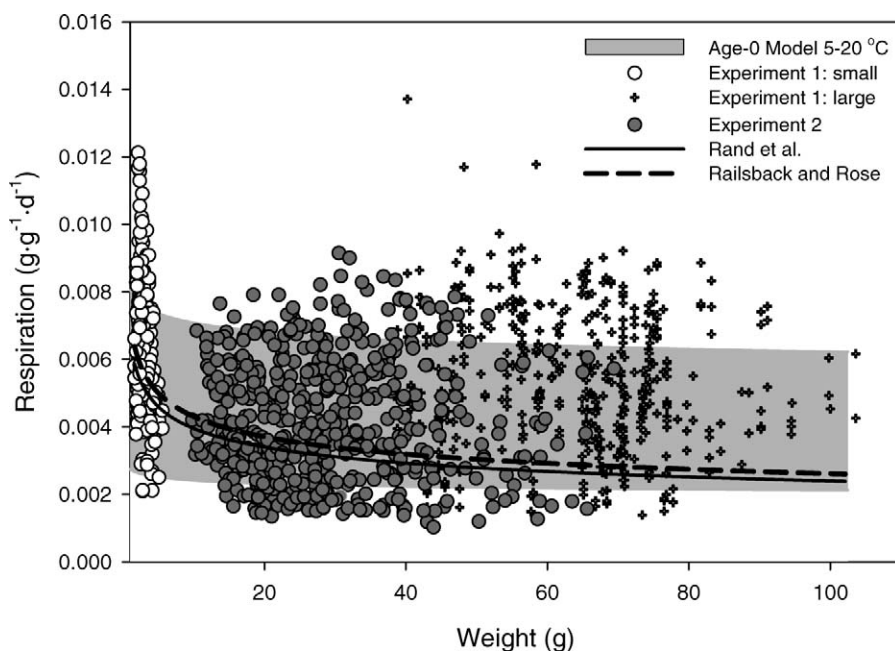


FIGURE 3.—Data and model predictions of the relationship between weight and the respiration rate of rainbow trout. The data are shown as individual points. The shaded region shows predictions from the new age-0 model over the temperature range 5–20°C. The predictions from the models of Rand et al. (1993) and Railsback and Rose (1999) use a temperature of 15°C.

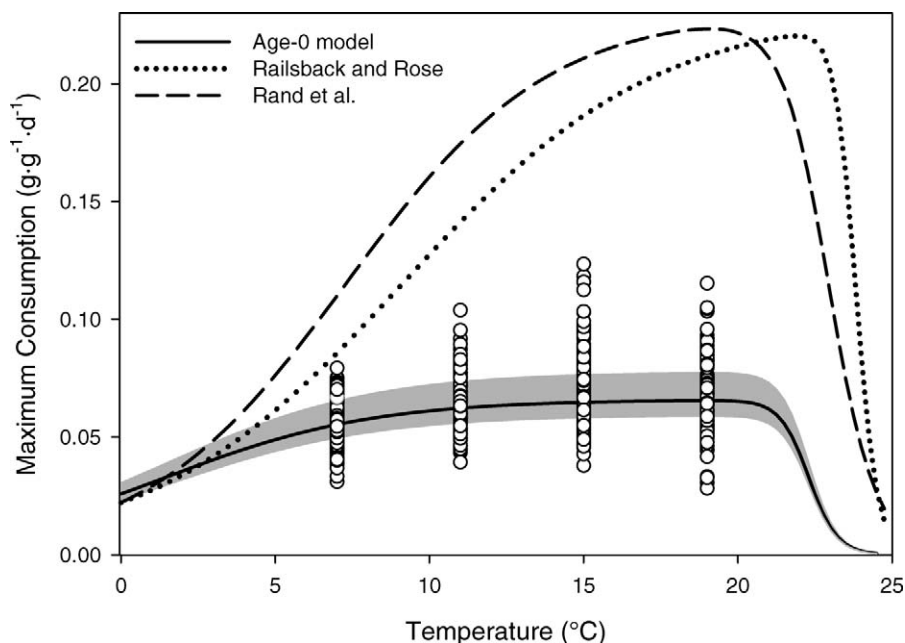


FIGURE 4.—Data and model predictions of the relationship between temperature and the maximum feed consumption rate of rainbow trout. The data are shown as individual points. The model predictions include those from the new age-0 model (the mean  $\pm$  SD are indicated by the solid line and the shaded area, respectively) and those from the models of Rand et al. (1993) and Railsback and Rose (1999). All predictions are based on the mean weight of the fish in experiment 2.

maximum consumption rates in the 10–20°C temperature range show notable differences in the adult model, but in both the data and the age-0 model, maximum consumption differs little in this temperature range.

### Discussion

The finding of a significant differences among individuals with respect to respiration and maximum feed consumption rates represents the most important result in this study. Previous studies measuring bioenergetic rates have shown large amounts of variation in rates (e.g., Stewart et al. 1983; Hartman and Brandt 1995; Myrick and Cech 1996) but focused on the overall population trend. Because these studies focused on population trends, they did not collect data that allowed for an analysis of individual differences in bioenergetic rates. Results of the repeated measures of respiration and maximum consumption in these experiments suggest that some of the variability observed in previous studies of bioenergetic rates may result from consistent and measurable differences between individuals.

Bioenergetic models of fish growth have played an important role in the development of individual-based fish population models (IBMs; DeAngelis and Gross 1992; Van Winkle et al. 1993 [and many other papers

in *Transactions of the American Fisheries Society* 122(3)]; Giske et al. 1998). To date, the IBMs of fish populations have assumed no difference among bioenergetic rates of individual fish because there were no data suggesting the presence of important, detectable differences among individuals of the same species and size-class. The results of experiments 1 and 2 show that differences in bioenergetic rates do exist among individual fish of the same species and size-class.

Dating back to some of the early models (e.g., DeAngelis et al. 1979), IBMs have consistently shown that small differences among individuals can have important effects on population survival and growth rates (DeAngelis et al. 1991; Rose and Cowan 1993; Rose et al. 1996). Our finding of significant individual differences in the key bioenergetic rates of maximum feed consumption and respiration suggests that these differences are important enough to be included in IBMs of fish populations. The overall effect of variability in bioenergetic rates on the predictions of fish population IBMs is, obviously, uncertain at present. However, because bioenergetic models play a central role in many IBMs, the effect of individual variation in these rates should be explored.

The period used to acclimate our fish to each water temperature (36 h minimum) differs from the acclima-



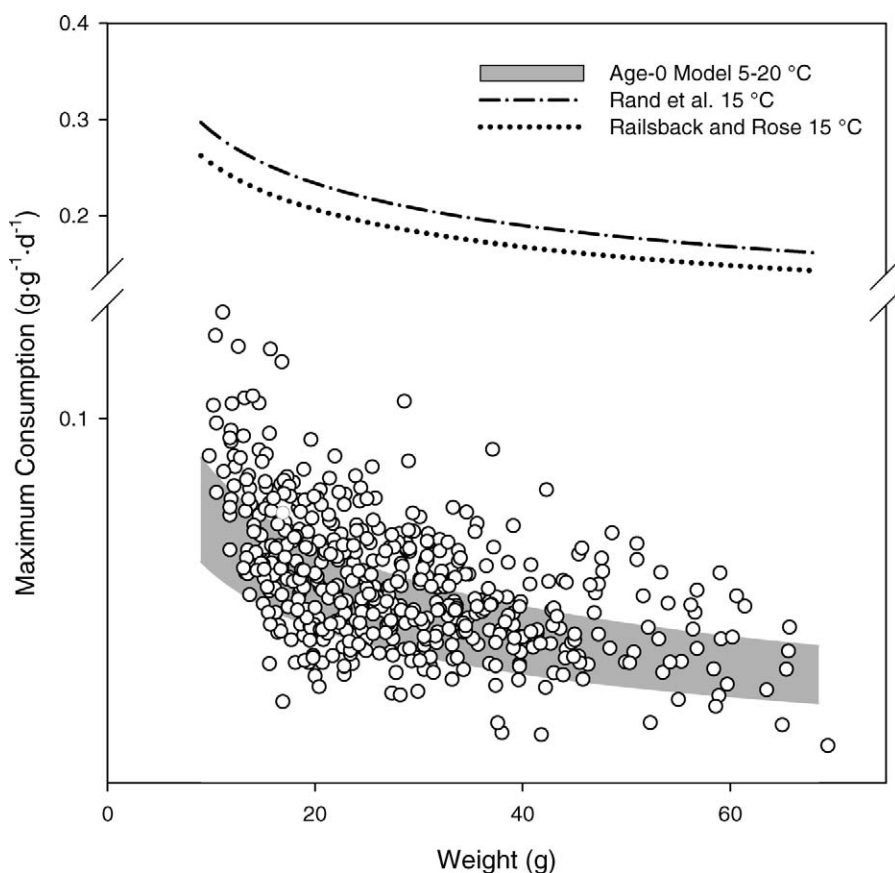


FIGURE 5.—Data and model predictions of the relationship between weight and the maximum feed consumption rate of rainbow trout. The data are shown as individual points. The shaded region shows the predictions from the new age-0 model over the temperature range 5–20°C. The predictions from the models of Rand et al. (1993) and Railsback and Rose (1999) use a temperature of 15°C.

tion period used in previous experiments. Rao (1968) acclimated rainbow trout to test water temperatures for a minimum of 2 weeks before collecting oxygen consumption data. In experiments on maximum consumption and respiration rates, Hartman and Brandt (1995) acclimated three marine species (striped bass *Morone saxatilis*, bluefish *Pomatomus saltatrix*, and weakfish *Cynoscion regalis*) to test temperatures for a minimum of 24 h. Stewart et al. (1983) acclimated lake trout *Salvelinus namaycush* for 48 h before collecting respiration data. We chose an acclimation period considerably shorter than that used by Rao (1968) and shorter than that used by Stewart et al. (1983) largely because fish experience changes in temperature over time scales of less than 48 h and considerably less than 2 weeks. Rainbow trout are likely to be well adapted to acclimate to water temperatures within periods of less than 1 d; thus, a 36-h acclimation period

seems appropriate and not as short that that used by Hartman and Brandt (1995).

In experiment 2 we measured maximum consumption from two feeding bouts in a single 24-h period. This approach is similar to that used in some previous experiments (Stewart et al. 1983; Hartman and Brandt 1995) but differs from that of ad libitum feeding used in other experiments (e.g., Hayward and Arnold 1996). We elected to use two feeding bouts in a 24-h period primarily for logistical reasons. The fish that we used in our experiments had fed only on commercial food their entire life; thus, we used a food very similar to the one they were fed in the hatchery. The feces of our fish were difficult to distinguish from the commercial food for final weighing. By limiting the feeding period to short bouts, we greatly reduced the amount of feces that had to be separated from the food, making removal of the feces easier and making final of weight the uneaten food more reliable.

Using the combined intake from two short feeding bouts to represent maximum consumption, as we did in experiment 2, may overestimate maximum feed consumption. Results from Hayward et al. (1997) show that fish consume much greater amounts of food in feeding periods that were immediately preceded by fasting. Their results suggest that ration size may be affected by the period since fasting. When fed ad libitum on the sixth day after fasting, fish consumed less than half of the food that they consumed on the first day after fasting (Hayward et al. 1997). Even though our experimental protocol may have overestimated maximum consumption (per Hayward et al. 1997), the values of maximum consumption from models for adults (Rand et al. 1993; Railsback and Rose 1999) were nearly four times our values for age-0 fish. Thus, an age-0 maximum consumption model that differs from the adult model is appropriate.

Our data allow us to create a new parameter set for the maximum feed consumption and respiration rate components of the Wisconsin bioenergetics model for age-0 rainbow trout. The predictions of the new model differ considerably from those of the models created for adult rainbow trout. The fact that bioenergetic rates differ by life stage is a common finding, as evidenced by the number of species for which different parameter sets have been developed for adults and young of year (see Hanson et al. 1997). We expect that the parameter set we present here for age-0 rainbow trout bioenergetics will prove useful because the species is widespread and supports valuable fisheries in many areas. We hope that our parameter set will enable more accurate models of age-0 rainbow trout growth or population dynamics to be developed.

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