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[Note]

Improvement of Bioenergetics Model Predictions for Fish Undergoing Compensatory Growth

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Abstract.—A previous evaluation of a bioenergetics model applied to juvenile hybrid sunfish (F_1 hybrid of female green sunfish *Lepomis cyanellus* × male bluegill *L. macrochirus*) undergoing compensatory growth (CG) indicated that the model substantially overestimated growth and underestimated cumulative consumption. This result suggested that fish bioenergetics models might not adequately account for physiological shifts that occur during CG. However, we demonstrate that application of a recently developed procedure for correcting consumption- and growth-rate-dependent systematic errors common among bioenergetics models negates much of the predictive error that had been attributed to the physiological complexities of CG. Correction equations for estimating the model-relative growth rate error (predicted less observed; $g \cdot g^{-1} \cdot d^{-1}$) from the observed mean daily consumption rate ($g \cdot g^{-1} \cdot d^{-1}$) and the consumption rate error (predicted less observed; $g \cdot g^{-1} \cdot d^{-1}$) from the observed relative growth rate ($g \cdot g^{-1} \cdot d^{-1}$) were derived by applying linear regression analysis to data from individual hybrid sunfish not undergoing CG. These independently generated correction equations significantly improved model predictions of growth and cumulative consumption for three groups of fish undergoing CG at one temperature near their growth optimum. The findings indicate that the high consumption and growth rates characteristic of fish undergoing CG merely amplify the consumption- and growth-rate-dependent errors inherent in bioenergetics models and that model predictions for fish undergoing CG can be significantly improved through application of the correction procedure.

Bioenergetics models have been constructed for at least 25 fish species and have been used with increasing frequency during recent years by fisheries scientists and managers to address a diverse array of issues (Hanson et al. 1997). One criticism of these models during the past decade has been a scarcity of independent evaluations of model performance (Ney 1993). However, several laboratory evaluations of fish bioenergetics models have been published during the past 8 years (e.g., Whitledge and Hayward 1997; Whitledge et al. 1998, 2003; Madenjian and O'Connor 1999; Chipps et al. 2000; Madenjian et al. 2000, 2004; Bajer et al. 2003) that have provided substantial new insights into model strengths and weaknesses. A recent analysis of data from laboratory evaluations of seven bioenergetics models (Bajer et al. 2004b) found that model errors for predicting fish growth rates were strongly correlated with observed mean daily food consumption rates. Significant associations between mean daily consumption and growth rate prediction errors have been reported for two additional models (Cui and Wootton 1989; Chipps et al. 2000), suggesting that consumption-dependent errors could be widespread among fish bioenergetics models.

A regression-based approach has recently been developed to correct bioenergetics model predictions for consumption-dependent and other systematic errors (Bajer et al. 2004a). This procedure uses empirically derived relationships between model prediction errors and model input variables (e.g., mean daily food consumption) to adjust model predictions of growth or consumption based on known values of those model input variables during a given time interval. Application of this correction approach significantly improved growth and consumption predictions of a bioenergetics model for white crappie *Pomoxis annularis* (Bajer et al. 2004a). One of the principle advantages of this procedure is that model predictions can be substantially improved without resorting to the time-consuming and labor-intensive process of collecting additional laboratory data required to refine model parameter values or equations.

A previously published laboratory evaluation of a bioenergetics model applied to juvenile hybrid sunfish (F_1 hybrid of female green sunfish *Lepomis cyanellus* × male bluegill *L. macrochirus*; Whitledge et al. 1998) indicated that the model fared

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well in predicting growth of fish fed ad libitum daily but significantly overestimated growth and underestimated cumulative consumption when applied to fish undergoing compensatory growth (CG); the magnitude of model error was positively related to the vigor of the CG response. Compensatory growth refers to an organism's capacity to grow at an accelerated rate after a period of food shortage or reproductive weight loss and can involve increases in food consumption rate (hyperphagia) and growth efficiency (Jobling 1994). Mechanisms responsible for model errors were unknown but were suspected to involve complex physiological responses particular to CG that were not accommodated by the bioenergetics model. However, a reexamination of data from Whitledge et al. (1998) discovered a significant positive correlation between mean daily food consumption rate and model growth prediction error that closely resembled model growth error–consumption rate relationships observed in other bioenergetics models (Bajer et al. 2004b). This suggests that error sources for growth predictions in the presence of CG were similar to those responsible for growth prediction errors under non-CG conditions and that model growth and consumption predictions for fish undergoing CG could potentially be improved with the regression-based correction approach of Bajer et al. (2004a). The objectives of this study were to evaluate whether consumption-dependent errors discovered in recent evaluations of bioenergetics models were responsible for poor growth predictions for hybrid sunfish undergoing CG (Whitledge et al. 1998) and to determine the extent to which application of the recently developed model-correcting procedure (Bajer et al. 2004a) could improve bioenergetics model growth and consumption predictions for juvenile hybrid sunfish that exhibited strong CG responses.

Methods

Compensatory growth experiment and previous model evaluation data.—Individual growth and daily food consumption data for 21 juvenile hybrid sunfish (initial live weight, 9.3–18.8 g) undergoing CG at 24 ± 1°C were obtained from Hayward et al. (1997). Each fish was fed mealworms *Tenebrio molitor* and subjected to one of three repeating no-feed and refeed regimes; no-feed periods were fixed at 2, 4, or 14 d (groups designated as D2, D4, and D14, respectively). Bioenergetics model predictions of final weights (g) and cumulative consumption (g) and model errors (%) for predicting final weights and cumulative consumption for individual fish in the Hayward et al. (1997) study were obtained from Whitledge et al. (1998).

Derivation of correction equations.—Equations relating model relative growth rate error ($\mathrm{RGR_{err}}$; predicted less observed relative growth rates; $\mathrm{g \cdot g\ initial\ weight^{-1} \cdot d^{-1}}$) to observed mean daily consumption rate ($\mathrm{g\ of\ food\ consumed \cdot g\ initial\ weight^{-1} \cdot d^{-1}}$) and model consumption rate error ($\mathrm{CR_{err}}$; predicted less observed consumption rates; $\mathrm{g \cdot g^{-1} \cdot d^{-1}}$) to observed relative growth rate ($\mathrm{g \cdot g^{-1} \cdot d^{-1}}$) were constructed to correct bioenergetics model growth and consumption predictions for hybrid sunfish undergoing CG. Data used to develop correction equations were independent of those on which corrections were applied. Consumption and growth data for deriving correction equations were obtained from 50 individually held hybrid sunfish (8.2–35.6 g wet weight) that were fed mealworms ad libitum daily at either 22°C or 24°C and were not undergoing CG (Hayward et al. 1997, 2000; G. W. Whitledge, unpublished data). Data from fish that exhibited CG were not used in the derivation of correction equations to test whether model prediction errors for hybrid sunfish undergoing CG could be significantly reduced solely by accounting for consumption- and growth rate-dependent errors that appear common among bioenergetics models (Bajer et al. 2004b). Thus, correction equations did not account for model errors associated with complex physiological changes particular to the CG response.

Body weight changes (g) and cumulative consumption (g) for individually held hybrid sunfish not undergoing CG that were used to develop correction equations were predicted with Bioenergetics 3.0 (Hanson et al. 1997). Physiological parameters, predator and prey energy densities, and activity (ACT) values were identical to those used in the previous model evaluation for hybrid sunfish (Whitledge et al. 1998). Least-squares linear regression was applied to relate model $\mathrm{RGR_{err}}$ to observed mean daily consumption rate and model $\mathrm{CR_{err}}$ to observed relative growth rate for individual fish. Significant associations between model $\mathrm{RGR_{err}}$ and mean daily consumption rate ($r^2 = 0.91$, $P < 0.001$) and between model $\mathrm{CR_{err}}$ and mean relative growth rate ($r^2 = 0.86$, $P < 0.001$) were detected. The resulting regression models ($\mathrm{RGR_{err}} = 0.7757 \times \text{mean daily consumption} - 0.0098$; $\mathrm{CR_{err}} = -0.8853 \times \text{mean relative growth rate} + 0.0032$) were subsequently used to correct model growth and consumption predictions for fish undergoing CG.

Bioenergetics modeling and application of cor-

rection equations.—Body weight changes (g) and cumulative food consumption (g) were predicted for individual hybrid sunfish in each of the three groups (D2, D4, and D14) that exhibited CG with Bioenergetics 3.0 (Hanson et al. 1997). Physiological parameters, predator and prey energy densities, and ACT values were identical to those used in the previous model evaluation for hybrid sunfish (Whitledge et al. 1998). Using observed values of cumulative food consumption (g), water temperature (°C), and initial body weight (g), body weight change (g) was predicted for individual fish during each no-feed and refeed period. Predicted body weights at the end of a given no-feed or refeed period served as initial weights for growth simulations in the following no-feed or refeed period. Using observed water temperature (°C) and weekly changes in body weight (g), cumulative food consumption (g) was predicted for individual fish.

The equation for predicting model RGR_{err} was applied to adjust model predictions of body weight change for individual fish during each no-feed or refeed period. Observed values of mean daily consumption rate (g of food consumed $\cdot$ g initial weight^{-1} $\cdot$ d^{-1}) for individual fish during each no-feed or refeed period were entered into the correction equation to estimate the model's RGR_{err} for each fish. Estimates of RGR_{err} were then subtracted from predicted RGRs for each fish during each no-feed or refeed period to obtain adjusted values for RGR. Adjusted RGR values were multiplied by initial fish weight for a given no-feed or refeed period and number of days during that same no-feed or refeed period to obtain corrected predictions of individual fish weights at the end of each no-feed or refeed period. In the model-correcting process, corrected predictions of individual fish body weights at the end of a given no-feed or refeed period served as initial weights for growth simulations in the following no-feed or refeed period.

The equation for predicting model CR_{err} was used to adjust model predictions of cumulative consumption throughout the 105-d experiment. Observed values of relative growth rate (g weight change $\cdot$ g mean body weight^{-1} $\cdot$ d^{-1}) for individual fish during each week of the experiment were entered into the correction equation to estimate the model's CR_{err} (g $\cdot$ g^{-1} $\cdot$ d^{-1}) for each fish. Estimates of CR_{err} were then subtracted from predicted food consumption rates (CR) for each fish during each week of the experiment to obtain adjusted values for CR. Adjusted CR values were multiplied by mean fish weight and then by 7 d to obtain corrected predictions of cumulative consumption by individual fish at the end of each week of the experiment. Corrected predictions of cumulative consumption during each week were then summed throughout the entire experiment to obtain overall cumulative consumption estimates for individual fish.

Analytical procedures.—The relative performance of corrected (this study) and uncorrected (Whitledge et al. 1998) models applied to hybrid sunfish undergoing CG was assessed with each model's error (%) for predicting fish weights and cumulative consumption on the final day of the experiment (day 105). Mean percent errors for predicting final weights and cumulative consumption for individual fish in each treatment group were calculated for corrected and uncorrected models as

$$\text{Error (\%)} = 100 \cdot (\text{PRED} - \text{OBS}) \cdot \text{OBS}^{-1},$$

where PRED is the predicted value of fish final weight (g) or cumulative consumption (g) and OBS is the corresponding observed value. Intermodel differences in mean percent errors for predicting final weights and cumulative consumption in each treatment group were assessed with paired *t*-tests.

Results and Discussion

Application of the regression-based correction procedure (Bajer et al. 2004a) substantially improved bioenergetics model predictions of hybrid sunfish final weights under three feeding regimes that elicited moderate to strong CG at a near-optimum temperature for growth. Mean percent errors for predicting final weights of fish in each treatment group were significantly lower (five- to eightfold lower) for the corrected model compared with the uncorrected model (paired *t*-tests, $P <$ 0.05; Table 1). Substantial improvement in model growth prediction ability was observed even in the treatment group (D2) that exhibited the most vigorous CG response and displayed significant growth overcompensation (growth in excess of control fish fed ad libitum daily). Thus, capacity for the correction approach to extend the range of conditions for which bioenergetics models can yield accurate growth predictions was clearly demonstrated.

The mean weights of fish in group D14 predicted by the corrected model tracked the trajectory of observed mean fish weights more closely than the predictions of the uncorrected model (Figure 1). Mean weights predicted by the corrected model on

TABLE 1.—Mean observed final weights (FW; g) and cumulative consumption (CC; g) of hybrid sunfish from groups D2, D4, and D14 (Hayward et al. 1997) and mean final weights (FW_P; g) and cumulative consumption (CC_P; g) of fish in the same groups predicted by the uncorrected bluegill bioenergetics model (Whitledge et al. 1998) and the corrected bioenergetics model. Mean percent errors for predicting final weights and cumulative consumption for fish in each group are shown for the corrected and uncorrected models. Asterisks indicate significantly lower mean percent errors among corrected and uncorrected models within each group (paired *t*-tests; $P < 0.05$) and $n = 7$ fish/group. Values in parentheses are SEs.

Treatment group	Observed		Uncorrected model				Corrected model			
	FW	CC	FW_P	Mean % error (SE)	CC_P	Mean % error (SE)	FW_P	Mean % error (SE)	CC_P	Mean % error (SE)
D2	32.7 (5.0)	48.7 (9.8)	44.6 (9.6)	37 (6.8)	36.7 (5.1)	25 (3.5)	34.1 (5.6)	4.3* (2.3)	45.5 (7.9)	5.6* (1.6)
D4	26.0 (4.4)	35.9 (9.2)	32.2 (8.8)	24 (6.2)	29.7 (4.6)	18 (3.8)	26.9 (4.1)	3.5* (2.6)	34.0 (6.9)	5.0* (1.9)
D14	26.8 (3.3)	38.8 (5.7)	34.5 (5.5)	29 (4.5)	30.7 (3.5)	21 (3.0)	25.3 (3.3)	5.6* (1.5)	36.0 (5.2)	7.2* (1.0)

the first and last days of each of the three no-feed and refeed periods in group D14 were within 1 SE of observed mean weights on four of six dates and were never more than 15% different from observed values. In contrast, mean weights predicted by the uncorrected model on these dates differed from observed mean weights by as much as 41% and were never within 1 SE of mean observed weights. Although the uncorrected model underestimated growth (overestimated weight loss) during periods of food deprivation, the magnitude of this error ($44.7\ \text{J} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) was much lower than the rate at which the model overestimated positive growth rates during ad libitum feeding periods (up to $208.5\ \text{J} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$). Thus, even the uncorrected model's tendency to underestimate growth during food deprivation did little to offset the substantial consumption rate-dependent errors that accrued in the presence of hyperphagia associated with CG. Predicted weights for groups D2 and D4 at the beginning and end of the no-feed and refeed periods could not be similarly evaluated, as weighing dates did not coincide with the beginning and end of the no-feed and refeed periods in these groups as they did in group D14.

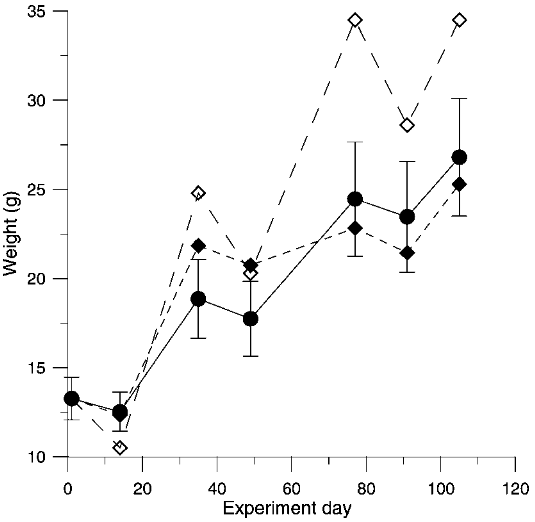

FIGURE 1.—Mean observed weights (g; ±SE) of hybrid sunfish in group D14 at the beginning and end of each no-feed and refeed cycle (circles) and the corresponding mean weights predicted by the corrected (solid diamonds) and uncorrected (open diamonds) bioenergetics models.

Results indicate that systematic errors associated with food consumption rate and periods of reduced resting metabolism discovered in recent evaluations of several bioenergetics models (Chipps et al. 2000; Bajer et al. 2004b) were responsible for poor model growth predictions for hybrid sunfish undergoing CG reported by Whitledge et al. (1998). Fish bioenergetics models typically underestimate growth at relatively low rations, perform best at moderate rations, and increasingly overestimate growth at relatively high consumption rates (Bajer et al. 2004b). Significant improvement in model growth prediction accuracy for fish undergoing CG was accomplished with an error-correcting equation developed from fish that were not in the CG state. This suggests that substantial growth overestimation reported by Whitledge et al. (1998) was primarily a result of consumption-dependent errors inherent within the bioenergetics model (Bajer et al. 2004b) that were merely amplified during hyperphagic episodes rather than the model's inability to accommodate more complex physiological changes particular to the CG response.

Application of the regression-based model-correcting procedure also significantly improved bioenergetics model predictions of cumulative consumption by hybrid sunfish in all groups that exhibited CG. Mean percent errors for predicting cumulative consumption for fish in each treatment group were significantly lower (three- to fivefold lower) for the corrected model compared with the uncorrected model (paired *t*-tests, $P < 0.05$; Table 1). Results indicate that substantial improvements in bioenergetics model predictions of consumptive demand by fish feeding and growing at high rates characteristic of CG are possible over periods of weeks to months upon application of the model correction procedure. However, it is unlikely that even corrected bioenergetics models will be capable of tracking the pronounced day-to-day changes in food consumption that are typically observed during hyperphagia (Whitledge and Hayward 1997).

Increased accuracy of growth and consumption predictions for fish undergoing CG has potential significance for bioenergetics model applications in aquaculture settings. Compensatory growth continues to be of considerable interest as a method for increasing fish growth rates, improving feed conversion efficiency, decreasing waste production, and employing more convenient feeding schedules (Chatakondi and Yant 2001; Nikki et al. 2004; Tian and Qin 2004). Optimal use of bioenergetics models in culture settings (Knights 1985) will probably require that models have the capacity to accurately forecast fish growth rates under feeding regimes designed to elicit and maximize CG.

The ability to accurately predict growth and consumption for fish undergoing CG is also of potential importance to field applications of bioenergetics models. The extent to which CG responses are manifested in noncaptive fish is unknown, although CG capacity is present in a variety of freshwater and marine species representing at least eight families (Tian and Qin 2004), as few as 2 d of food deprivation are needed to elicit vigorous CG (Hayward et al. 1997), and complete cessation of feeding is not required to trigger CG (Miglavs and Jobling 1989; Russell and Wootton 1992; Bull and Metcalfe 1997; Whitledge, unpublished data). Periods of submaintenance feeding that could trigger CG have been documented for fish in a variety of environments; subsequent periods of substantially increased feeding rates and high day-to-day variation in food consumption that would be expected in the presence of CG have also been noted (Hayward and Margraf 1987; Weiland and Hayward 1997; Whitledge and Hayward 2000). Application of the bioenergetics model correction procedure is suggested when submaintenance feeding conditions juxtaposed with periods of relatively high prey availability are known or suspected to be occurring. Such conditions would yield substantial modeling error if the correction procedure is not applied. We anticipate that new equations will need to be developed when applying this correction procedure to bioenergetics model simulations for fish exhibiting CG under conditions distinct from those described in this paper (different species, fish sizes, or temperatures).

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