Transactions of the American Fisheries Society

Effects of Activity and Energy Budget Balancing Algorithm on Laboratory Performance of a Fish Bioenergetics Model

Charles P. Madenjian [a] , Solomon R. David [b] & Steven A. Pothoven [c]

[a] U.S. Geological Survey, Great Lakes Science Center, 1451 Green Road, Ann Arbor, Michigan, 48105, USA

[b] School of Natural Resources and Environment, , University of Michigan, 440 Church Street, Ann Arbor, Michigan, 48109, USA

[c] National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, Lake Michigan Field Station, 1431 Beach Street, Muskegon, Michigan, 49441, USA

PLEASE SCROLL DOWN FOR ARTICLE

ARTICLE

Effects of Activity and Energy Budget Balancing Algorithm on Laboratory Performance of a Fish Bioenergetics Model

Charles P. Madenjian*

U.S. Geological Survey, Great Lakes Science Center, 1451 Green Road, Ann Arbor, Michigan 48105, USA

Solomon R. David

School of Natural Resources and Environment, University of Michigan, 440 Church Street, Ann Arbor, Michigan 48109, USA

Steven A. Pothoven

National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, Lake Michigan Field Station, 1431 Beach Street, Muskegon, Michigan 49441, USA

Abstract

We evaluated the performance of the Wisconsin bioenergetics model for lake trout *Salvelinus namaycush* that were fed ad libitum in laboratory tanks under regimes of low activity and high activity. In addition, we compared model performance under two different model algorithms: (1) balancing the lake trout energy budget on day *t* based on lake trout energy density on day *t* and (2) balancing the lake trout energy budget on day *t* based on lake trout energy density on day *t* + 1. Results indicated that the model significantly underestimated consumption for both inactive and active lake trout when algorithm 1 was used and that the degree of underestimation was similar for the two activity levels. In contrast, model performance substantially improved when using algorithm 2, as no detectable bias was found in model predictions of consumption for inactive fish and only a slight degree of overestimation was detected for active fish. The energy budget was accurately balanced by using algorithm 2 but not by using algorithm 1. Based on the results of this study, we recommend the use of algorithm 2 to estimate food consumption by fish in the field. Our study results highlight the importance of accurately accounting for changes in fish energy density when balancing the energy budget; furthermore, these results have implications for the science of evaluating fish bioenergetics model performance and for more accurate estimation of food consumption by fish in the field when fish energy density undergoes relatively rapid changes.

Fish bioenergetics models have frequently been applied to problems and issues in fishery science (Hansen et al. 1993; Bajer et al. 2004; Madenjian 2011). Bioenergetics modeling has been instrumental in estimating the strength of the predator–prey trophic link in food webs (Madenjian 2011). For example, Stewart et al. (1981) developed bioenergetics models for salmon and trout and then applied these models to populations in Lake Michigan. Results indicated that each year, the salmonine populations were consuming as much as 33% of the annual pro-duction of alewives *Alosa pseudoharengus*, the favored prey of the salmonines in Lake Michigan. Stewart et al. (1981) warned fishery managers that the alewife population was headed for a collapse due to predation by salmonines. Heeding the warning, fishery managers began reducing the stocking rates of Chinook salmon *Oncorhynchus tshawytscha* into Lake Michigan during the 1980s (Hansen et al. 1993), and stocking reductions have continued through the 1990s and 2000s (Bence and Smith 1999; Claramunt et al. 2009). Bioenergetics modeling has also been

used to assess the effects of various factors on fish growth in lakes (Hayward and Margraf 1987; Madenjian et al. 1998), to assess the role of phosphorus excretion by fish populations in the phosphorus cycling within aquatic ecosystems (Kraft 1993; Bunnell et al. 2005), and to identify the major factors regulating contaminant accumulation in fish (Weininger 1978; Stow et al. 1995).

Despite frequent applications of fish bioenergetics models to fisheries problems, few evaluations of bioenergetics model performance were conducted prior to 1993 (Hansen et al. 1993; Ney 1993). Both Hansen et al. (1993) and Ney (1993) agreed that further testing and evaluation of fish bioenergetics models were needed. Evaluations of fish bioenergetics models, both in the laboratory and in the field, have ensued (Bajer et al. 2003; Chipps and Wahl 2004; Lantry et al. 2008).

Based on results from these fish bioenergetics model evaluations, Bajer et al. (2004) concluded that fish bioenergetics models contained a consumption-dependent systematic error that would cause the models to underestimate consumption when feeding rates were relatively high. These researchers reasoned that the bias was likely due to inaccurate submodels for energy budget components associated with feeding rate. Egestion, excretion, and specific dynamic action (SDA) have typically been modeled as functions of feeding rate in most fish bioenergetics models. Bajer et al. (2004) recommended that additional laboratory work be conducted to measure egestion, excretion, and SDA over broad ranges of consumption level, fish body weight, temperature, and prey type.

Based on findings by Christiansen and Jobling (1990), Madenjian and O'Connor (1999) suggested that fish bioenergetics models' underestimation of consumption at high feeding rates might be an artifact of fish being confined to a laboratory tank and thus having limited swimming activity. Arctic char *Salvelinus alpinus* that were exercised in laboratory tanks exhibited higher gross growth efficiencies (GGEs) than relatively inactive Arctic char (Christiansen and Jobling 1990), and these results indicated that the resting metabolic rate of the inactive fish was actually higher than that of the active fish. To test this idea, Madenjian and O'Connor (1999) proposed that bioenergetics model performance be evaluated in the laboratory for both active and inactive lake trout *S. namaycush* fed an ad libitum ration.

Another factor potentially influencing the laboratory performance of fish bioenergetics models was the model algorithm used to balance the fish's energy budget. To balance the energy budget on day t, Hanson et al. (1997) based their calculations on the fish's energy density on day t (algorithm 1). However, Hewett and Johnson (1987) used the fish's energy density on day $t + 1$ to balance the fish's energy budget on day t (algorithm 2). For the case of a constant fish energy density over time, the two algorithms will yield identical results. However, if the energy density of the fish changes over time, then the two algorithms will yield different results.

The overall goal of this study was to determine whether the effects of fish activity and energy budget balancing algorithm could be responsible for the above-mentioned underestimation of consumption by fish that are fed at a relatively high rate in the laboratory. The specific objective of the study was to determine whether significant bias could be detected in Wisconsin bioenergetics model predictions of consumption and growth based on algorithms 1 and 2 for lake trout at two activity levels (inactive and active) in laboratory tanks. The implications of our findings with regard to fish bioenergetics model evaluation are discussed. We also discuss the importance of properly accounting for changes in fish energy density while generating estimates of food consumption by fish in the field when fish energy density is undergoing relatively rapid changes.

METHODS

Laboratory experiment.—The laboratory experiment was conducted during 16 February–1 July 2010. Lake trout of the Seneca Lake strain were obtained from the Sullivan Creek National Fish Hatchery (U.S. Fish and Wildlife Service, Brimley, Michigan) in September 2009, when average weight of the fish was approximately 600 g (age = 44 months). The fish were fed pelletized commercial trout food at the hatchery, and we continued to administer the same diet during September through November 2009. Beginning in December 2009, the lake trout were acclimated to a diet of bloaters *Coregonus hoyi*, and the acclimation period continued through 15 February 2010. The bloater was selected as the food source because this species has served as a native prey for lake trout in the Laurentian Great Lakes (Madenjian et al. 1998).

Lake trout were maintained in iron-filtered well water at the Great Lakes Science Center in four 2,380-L circular fiberglass tanks (tanks 1–4; water exchange rate = 15 L/min) and four 870-L circular fiberglass tanks (tanks 5–8; water exchange rate = 5 L/min). Using centrifugal pumps, average water velocities in tanks 1–4 were maintained at 16.1, 17.1, 14.4, and 15.6 cm/s, respectively, based on readings from 36 locations in each tank (i.e., used to yield an overall average velocity for each tank). Average water velocities in tanks 5–8 were 2.9, 1.2, 2.1, and 1.5 cm/s, respectively, based on readings from 16 locations in each tank. This contrast in water velocities between the two treatments was selected based on the findings of Christiansen and Jobling (1990), who observed higher GGEs in Arctic char that were subjected to 13–26-cm/s water velocities than in fish that were subjected to 0–7-cm/s water velocities. Ambient well water temperature ranged from 11°C to 13°C, but we used chillers to maintain the water temperature between 8.3°C and 10.0°C, which coincided with the preferred water temperature range for lake trout in the Laurentian Great Lakes (Stewart et al. 1983; Bergstedt et al. 2003). Photoperiod was controlled with fluorescent lighting, which was adjusted seasonally to mimic the duration of daylight for the Laurentian Great Lakes region.

The number of lake trout placed into each tank was 19 fish for tanks 1 and 2; 18 fish for tanks 3 and 4; 14 fish for tanks 5 and 6; 16 fish for tank 7; and 15 fish for tank 8. Each lake trout was weighed on 16 February (the start of the experiment), 24 March, 26 April, 1 June, and 1 July 2010 (the end of the experiment). Lake trout were fed thawed bloaters, which had been caught in Lake Michigan during September 2009 and May 2010, frozen, and stored at $-30°C$. After thawing, bloaters were cut into pieces, with each piece being between 1 and 5 g in weight. Lake trout in all tanks were fed as much as they would consume during one feeding each day. We chose the ad libitum feeding level because we wanted to test the hypothesis proposed by Madenjian and O'Connor (1999) that fish activity has an effect on bioenergetics model performance for fish that are fed an ad libitum ration. Any food that was not consumed by the lake trout within 1 h after placement into the tank was removed, air dried for about 15 min, and weighed to the nearest 0.1 g.

At the start of the experiment, a subsample of fish was sacrificed from each tank (tanks 1 and 2: $n = 9$; tanks 3 and 4: $n = 8$; tanks 5 and 6: $n = 4$; tank 7: $n = 6$; tank 8: $n = 5$) and stored in plastic bags at $-30°C$ until further processing. All of the 10 lake trout remaining in each tank at the conclusion of the experiment were frozen at $-30°C$ until further processing. Additionally, 10 three-fish composite subsamples of bloaters caught during September 2009 and 10 six-fish composite subsamples of bloaters caught during May 2010 were stored at $-30°C$ for later analysis. More fish were included in the composite subsamples from May because those bloaters were substantially smaller than the bloaters that were caught during September. To determine energy density, lake trout were composited by stage (start or end of experiment) and tank. Each composite (lake trout or bloater) was homogenized in a blender. A 20–30-g portion of each mixture was oven dried for approximately 60 h at 70°C, and energy density was determined for a 1-g subsample of the dried material by using a Parr Model 1261 isoperibol calorimeter.

We calculated the GGE for each tank by subtracting the average weight of lake trout in the tank at the start of the experiment from the average weight of lake trout in the tank at the end of the experiment and then dividing this difference by the average amount of food eaten by a lake trout in the tank during the course of the 135-d experiment. To determine whether GGE differed significantly between the two fish activity levels, a two-sample t-test was applied to the GGE estimates; the GGE estimates for tanks 5–8 served as four low-activity replicates, and the estimates for tanks 1–4 served as four high-activity replicates.

Bioenergetics modeling.—A bioenergetics model for lake trout was developed by Stewart et al. (1983). This model is one of a set of fish bioenergetics models that are commonly referred to as Wisconsin bioenergetics models, as most models were developed by researchers at the University of Wisconsin. We applied the Stewart et al. (1983) model for lake trout to the growth and consumption data from our laboratory experiment. Inputs to the model included (1) water temperature regime experienced by lake trout in the laboratory tanks, (2) diet composition (wet weight basis) of the lake trout during the experiment, (3) energy densities of bloaters that were fed to the lake trout, and (4) energy densities of the lake trout during the experiment. Thus, our application was slightly different than that used by Stewart et al. (1983) for Lake Michigan lake trout. Rather than estimating energy density of lake trout as a function of lake trout weight per Stewart et al. (1983), we used the initial and final energy densities of lake trout (by tank) as inputs into the bioenergetics model. Predator energy density was linearly interpolated over time between the start and completion of the experiment. In addition, we assumed that lake trout maintained their position within the water flow of the tank; this same assumption was made by Madenjian and O'Connor (1999) in an earlier laboratory evaluation of the lake trout bioenergetics model. Based on visual observations of lake trout in tanks at various times of the day, this assumption appeared to be reasonable. Thus, even though the stocking density (number of lake trout per m^3 of water) in the smaller tanks was nearly three times higher than that in the larger tanks, this difference in stocking density between the two tank sizes did not appear to have an additional influence on lake trout behavior and activity. For bioenergetics modeling purposes, we simulated lake trout at a constant swimming speed equal to the average flow rate within each tank.

We followed the procedure of Madenjian and O'Connor (1999) and used the bioenergetics model in two ways: (1) to predict consumption given the observed starting and ending average weights of lake trout over time interval t and (2) to predict growth given the starting average weight of the lake trout and the observed average consumption over time interval t. Predictions were generated for each test period ($t =$ about 1 month) and for the entire duration of the experiment ($t = 135$ d). All predictions were made on a tank-by-tank basis.

To generate predictions based on algorithm 1, we used the most recent version of the Wisconsin bioenergetics model software (Hanson et al. 1997). According to algorithm 1, the weight of a fish at the start of day $t + 1$, W_{t+1} (g), is calculated as

$$W_{t+1} = \frac{E_t + (ED_t W_t)}{ED_t}, \qquad (1)$$

where $E_t =$ net energy (J) gained from the food eaten by the fish during day t, $ED_t =$ energy density (J/g wet weight) of the fish at the start of day t, and $W_t =$ fish weight (g) at the start of day t. To calculate E_t, the sum of the energy allocated to metabolism, egestion, and excretion on day t is subtracted from the energy contained in the food that was consumed on day t. The energy contained in the fish at the end of day t is equal to E_t plus the product of ED_t and W_t. Thus, based on algorithm 1, the weight of the fish at the start of day $t + 1$ is calculated by dividing the energy contained in the fish at the end of day t by the energy density of the fish at the start of day t.

To generate predictions based on algorithm 2, we developed and used a computer program written in PASCAL. According

to algorithm 2, W_{t+1} is calculated by

$$W_{t+1} = \frac{E_t + (ED_t W_t)}{ED_{t+1}}, \qquad (2)$$

where ED_{t+1} = energy density (J/g wet weight) of the fish at the start of day $t + 1$. Thus, based on algorithm 2, the fish's weight at the start of day $t + 1$ is calculated by dividing the energy contained in the fish at the end of day t by the energy density of the fish at the start of day $t + 1$. Equation (2) correctly expresses the conservation of energy because to accurately balance a fish's energy budget, the energy contained in the fish at the start of day $t + 1$ (i.e., $W_{t+1} \times ED_{t+1}$) must equal the energy contained in the fish at the start of day t (i.e., $W_t \times ED_t$) plus the net energy gained from the food eaten by the fish during day t. Multiplication of both sides of equation (2) by ED_{t+1} reveals that the use of algorithm 2 leads to an accurate balancing of the energy budget.

Evaluation of bioenergetics model predictions.—To investigate the effects of activity and energy budget balancing algorithm on bioenergetics model performance, we evaluated four sets of monthly predictions of the lake trout bioenergetics model: (1) model predictions based on algorithm 1 for inactive fish (tanks 5–8); (2) predictions based on algorithm 1 for active fish (tanks 1–4); (3) predictions based on algorithm 2 for inactive fish; and (4) predictions based on algorithm 2 for active fish.

We evaluated each set of monthly predictions from the lake trout bioenergetics model in a manner similar to that used by Madenjian and O'Connor (1999). First, we used a *t*-test for paired comparisons to determine whether the average difference between observed and predicted consumption was significantly different from 0. An average difference that was significantly different from 0 would indicate significant bias in the model predictions. For our application, we subtracted the predicted value from the observed value. In addition, we performed simple linear regression analysis for the predicted values as a function of observed values. If the model predictions were unbiased, then the slope of the regression line would not differ significantly from 1.0 and the intercept of the regression line would not differ significantly from 0. Bonferroni 95% joint confidence intervals were constructed to test the null hypotheses that the slope was equal to 1.0 and the intercept was equal to 0 (Neter et al. 1983). We applied these statistical analyses to the sets of observations and model predictions for monthly consumption and lake trout weight at the end of the monthly test period. As was explained by Madenjian and O'Connor (1999), we expected that in some instances, the paired *t*-test would be more powerful at detecting bias, whereas in other cases the linear regression analysis would be the more powerful approach. Using the portmanteau test (Madenjian and O'Connor 1999), we failed to detect significant autocorrelation in (1) the residuals from the regression analyses, (2) the differences between observed and predicted consumption, or (3) the differences between observed and predicted final weight. Consequently, we did not expect that re-

sults from our statistical testing would be confounded by serial correlation.

We used two-way ANOVA to determine significance of the effects of activity and energy budget balancing algorithm on the accuracy of the bioenergetics model's 135-d predictions. First, we formed the ratio of predicted : observed cumulative consumption for each tank over the entire 135-d experiment. We then calculated the percent deviation from observed cumulative consumption by taking the absolute value of the difference between this ratio and 1. A two-way ANOVA was then applied to the percent deviation values, with activity and energy budget balancing algorithm as the main effects; the interaction term was also included in the ANOVA model. In a manner analogous to that used for cumulative consumption, we formed the ratio of predicted : observed final weight of lake trout over the 135-d experiment to evaluate the bioenergetics model's predictions for growth. The percent deviation between observed and predicted final weights was calculated by taking the absolute value of the difference between this ratio and 1. A two-way ANOVA, with activity and energy budget balancing algorithm as the main effects and the interaction term included, was applied to the percent deviation values to assess the significance of the main effects for the accuracy of model-predicted cumulative growth over the entire experiment. We set α equal to 0.05 for all statistical testing.

RESULTS

Energy density of lake trout increased in all eight tanks during the experiment. Initial energy densities were 8,585 J/g (wet weight basis) for tank 1; 8,417 J/g for tank 2; 8,101 J/g for tank 3; 9,044 J/g for tank 4; 9,059 J/g for tank 5; 8,671 J/g for tank 6; 8,564 J/g for tank 7; and 8,326 J/g for tank 8. Final energy densities were 10,011 J/g for tank 1; 10,708 J/g for tank 2; 10,904 J/g for tank 3; 10,664 J/g for tank 4; 10,311 J/g for tank 5; 9,285 J/g for tank 6; 9,931 J/g for tank 7; and 10,040 J/g for tank 8. Energy densities of the 10 subsamples of bloaters caught during September ranged from 6,334 to 8,971 J/g, with a mean of 7,871 J/g and SE of 246 J/g. Energy densities of the 10 subsamples of bloaters captured in May ranged from 4,470 to 6,327 J/g, with a mean of 5,479 J/g and SE of 181 J/g.

The GGEs for the eight tanks ranged from 0.194 to 0.293 (Table 1). Mean GGEs for the high-activity and low-activity lake trout were 0.261 and 0.251, respectively. The difference in mean GGE between the two activity levels was not significant (*t*-test: $t = -0.41$, df = 6, $P = 0.6974$).

When algorithm 1 (equation 1) was used to balance the energy budget, the bioenergetics model significantly underestimated monthly consumption for both inactive and active lake trout. For inactive lake trout, results from a paired *t*-test revealed that the mean difference between observed and predicted monthly consumption was significantly greater than 0 (Table 2). Furthermore, the slope of the regression line of predicted monthly consumption as a function of observed monthly

TABLE 1. Observed and predicted cumulative consumption and cumulative growth by an average lake trout in laboratory tanks (4 tanks per activity level: active or inactive). The experiment was run for 135 d, and the lake trout were fed bloaters. Inactive lake trout were subjected to an average flow rate of 1.9 cm/s, and active lake trout were subjected to an average flow rate of 15.8 cm/s. Observed consumption is the total amount of food eaten by all fish in the tank divided by the number of fish in the tank. Gross growth efficiency (GGE) is the lake trout weight gain divided by the amount of food consumed. For algorithm 1, the energy budget of the lake trout for day t was balanced by using the lake trout energy density on day t. For algorithm 2, the energy budget of the lake trout for day t was balanced by using the energy density on day $t + 1$. The lake trout bioenergetics model developed by Stewart et al. (1983) was used to generate predictions of consumption and growth.

Characteristic	Inactive lake trout				Active lake trout			
	Tank 5	Tank 6	Tank 7	Tank 8	Tank 1	Tank 2	Tank 3	Tank 4
Observed consumption and growth								
Initial weight (g)	694	729	754	729	907	860	890	817
Final weight (g)	1,242	853	1,050	1,092	1,345	1,339	1,518	1,566
Consumption (g)	1,870	641	1,203	1,336	1,734	1,999	2,344	2,649
GGE	0.293	0.194	0.246	0.272	0.252	0.240	0.268	0.283
Predicted consumption and growth based on algorithm 1								
Consumption (g)	1,518	553	942	1,060	1,469	1,596	1,883	2,230
Final weight (g)	1,394	897	1,173	1,222	1,464	1,513	1,715	1,733
Ratio of predicted to observed consumption	0.812	0.863	0.783	0.793	0.847	0.799	0.803	0.842
Ratio of predicted to observed final weight	1.122	1.051	1.117	1.119	1.089	1.130	1.129	1.107
Predicted consumption and growth based on algorithm 2								
Consumption (g)	1,794	654	1,207	1,403	1,824	2,169	2,682	2,693
Final weight (g)	1,272	847	1,048	1,064	1,307	1,276	1,397	1,550
Ratio of predicted to observed consumption	0.960	1.021	1.003	1.050	1.052	1.086	1.144	1.017
Ratio of predicted to observed final weight	1.024	0.992	0.998	0.974	0.972	0.952	0.920	0.990

TABLE 2. Statistical comparison of predicted and observed consumption and growth of lake trout (two activity levels: active and inactive) during a laboratory experiment used to evaluate a lake trout bioenergetics model (N = number of pairs of data). Predictions were based on the model developed by Stewart et al. (1983) and used either algorithm 1 (equation 1) or algorithm 2 (equation 2). Inactive lake trout were subjected to an average flow rate of 1.9 cm/s, and active lake trout were subjected to an average flow rate of 15.8 cm/s. The model was evaluated for its predictions of (1) consumption during a test period of roughly 1 month and (2) weight at the end of a monthly test period. Paired t-tests were used to determine whether the average difference between values (observed value − predicted value) was significantly different from 0. Regression analyses of predicted values as a linear function of observed values were also performed; Bonferroni joint 95% confidence intervals (95% CIs) are shown for the null hypotheses that the intercept (β_0) is equal to 0 and the slope (β_1) is equal to 1.0.

| Activity level	Algorithm	N	Mean difference (g)	Attained P for paired t-test	$\beta_0 \pm$ 95% CI (g)	$\beta_1 \pm$ 95% CI
Food consumption during the test period						
Inactive	1	16	60.8	< 0.0001	20.6 ± 44.2	0.74 ± 0.13
Active	1	16	97.7	< 0.0001	51.8 ± 101.4	0.73 ± 0.18
Inactive	2	16	−0.7	0.9429	41.3 ± 60.8	0.87 ± 0.18
Active	2	16	−40.6	0.0058	77.7 ± 163.3	0.93 ± 0.29
Weight at the end of the test period						
Inactive	1	16	−29.9	< 0.0001	15.1 ± 84.9	1.02 ± 0.09
Active	1	16	−43.5	< 0.0001	42.7 ± 86.6	1.00 ± 0.07
Inactive	2	16	−0.2	0.9698	25.6 ± 69.7	0.97 ± 0.07
Active	2	16	16.4	0.0033	11.1 ± 84.0	0.98 ± 0.07
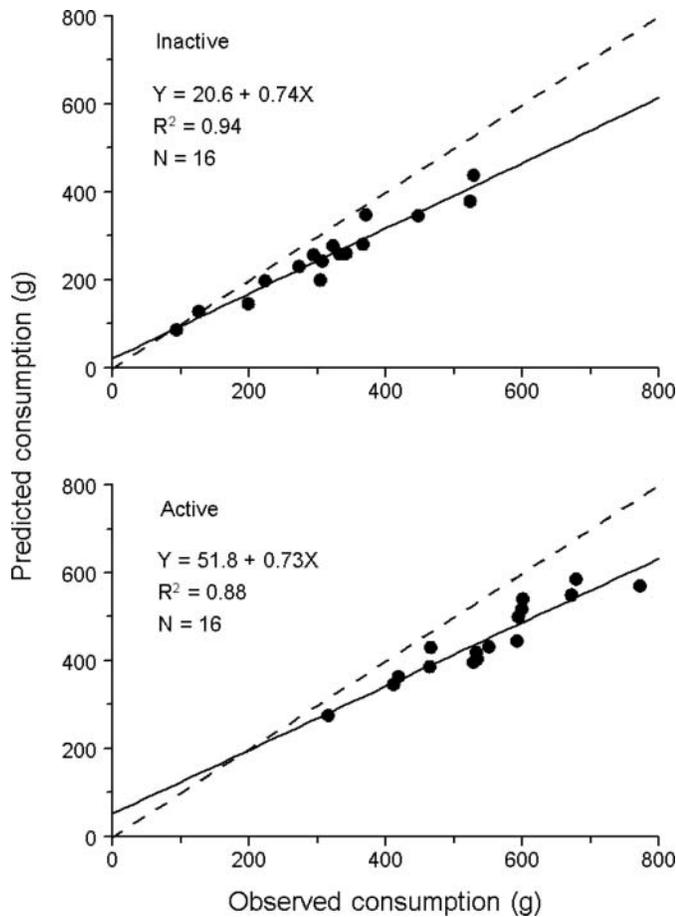
FIGURE 1. Predicted versus observed consumption by an average lake trout in a test tank at two fish activity levels (inactive [average flow rate = 1.9 cm/s] and active [15.8 cm/s]; 4 tanks for each activity level) during each test period (~1 month long; 4 periods/tank). Predictions were made with the bioenergetics model developed by Stewart et al. (1983) and with algorithm 1 (balancing of the energy budget on day t by using lake trout energy density on day t); the model was applied to each combination of tank and test period. The solid line represents the regression line fitted to the points; the dashed line represents the line of 1:1 correspondence between predictions and observations.
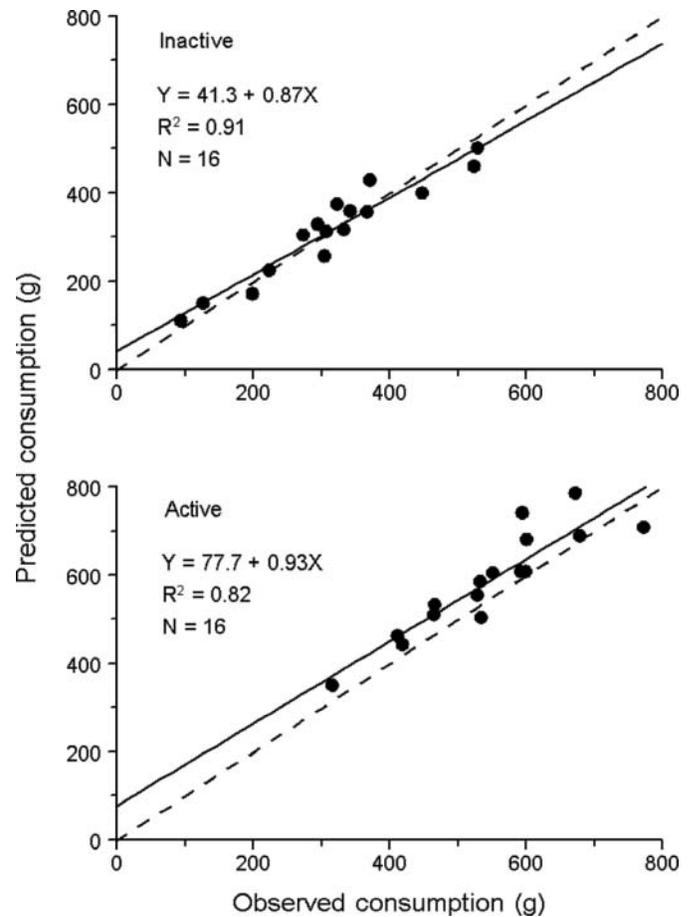
FIGURE 2. Predicted versus observed consumption by an average lake trout in a test tank at two fish activity levels (inactive [average flow rate = 1.9 cm/s] and active [15.8 cm/s]; 4 tanks for each activity level) during each test period (~1 month long; 4 periods/tank). Predictions were made with the bioenergetics model developed by Stewart et al. (1983) and with algorithm 2 (balancing of the energy budget on day t by using lake trout energy density on day $t + 1$); the model was applied to each combination of tank and test period. The solid line represents the regression line fitted to the points; the dashed line represents the line of 1:1 correspondence between predictions and observations.

consumption was significantly less than 1.0 (Table 2; Figure 1). Similar to the results for inactive lake trout, the mean difference between observed and predicted monthly consumption for active lake trout was significantly greater than 0 (Table 2). Moreover, the slope of the regression line of predicted versus observed monthly consumption was significantly less than 1.0 (Table 2; Figure 1). The degree of underestimation of monthly consumption was similar between the inactive and active lake trout (Figure 1).

When algorithm 2 (equation 2) was used to balance the energy budget, the bioenergetics model predictions of monthly consumption were unbiased for inactive lake trout and slightly biased for active lake trout. Paired t-test results indicated that model predictions were unbiased for inactive lake trout (Table 2). Further, for inactive lake trout, the slope of the regression line of predicted monthly consumption as a function of

observed monthly consumption was not significantly different from 1.0, and the intercept was not significantly different from 0 (Table 2; Figure 2). According to paired t-test results for active lake trout, the model slightly overestimated monthly consumption for these fish (Table 2). However, regression analysis did not show significant bias in the model predictions of monthly consumption by active lake trout (Table 2). Overall, model predictions of monthly consumption were more accurate when using algorithm 2 than when using algorithm 1 (Figures 1, 2).

When algorithm 1 was used to balance the energy budget, the paired t-test detected a significant bias in the bioenergetics model's predictions of weight at the end of a monthly test period for both inactive and active lake trout, whereas regression analysis failed to reveal a significant bias in the model predictions. Paired t-test results indicated a significant overestimation
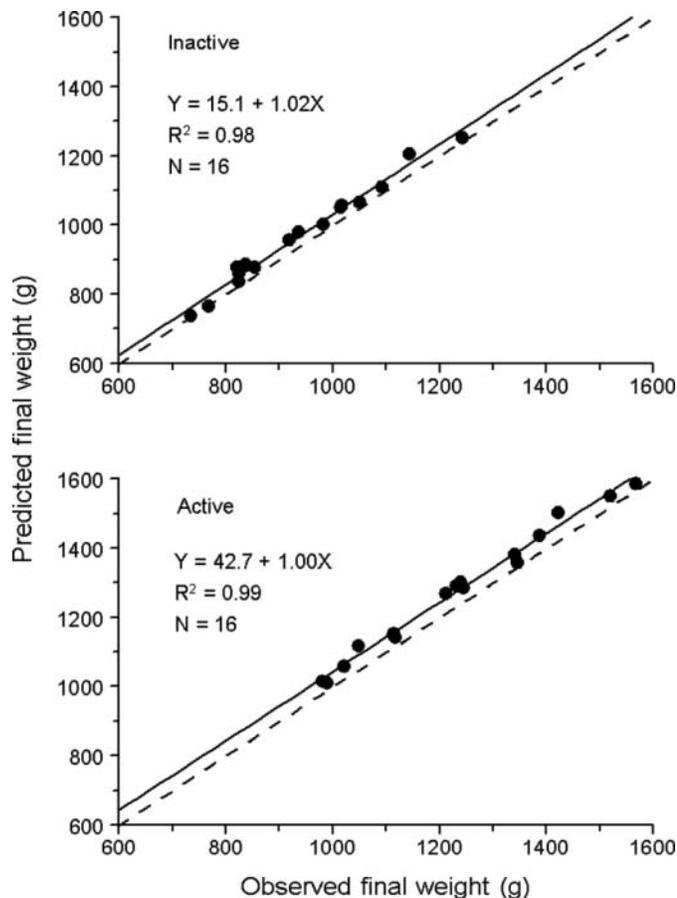
FIGURE 3. Predicted versus observed final weight at the end of each test period (~1 month long) for an average lake trout in a test tank at two fish activity levels (inactive [average flow rate = 1.9 cm/s] and active [15.8 cm/s]; 4 tanks for each activity level; 4 periods/tank). Predictions were made with the bioenergetics model developed by Stewart et al. (1983) and with algorithm 1 (balancing of the energy budget on day t by using lake trout energy density on day t); the model was applied to each combination of tank and test period. The solid line represents the regression line fitted to the points; the dashed line represents the line of 1:1 correspondence between predictions and observations.
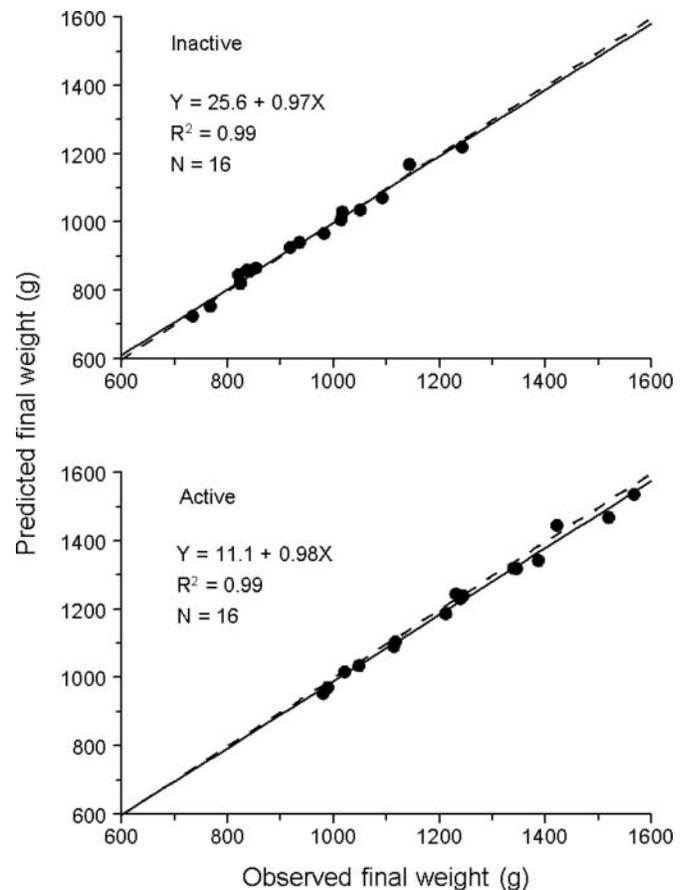

FIGURE 4. Predicted versus observed final weight at the end of each test period (~1 month long) for an average lake trout in a test tank at two fish activity levels (inactive [average flow rate = 1.9 cm/s] and active [15.8 cm/s]; 4 tanks for each activity level; 4 periods/tank). Predictions were made with the bioenergetics model developed by Stewart et al. (1983) and with algorithm 2 (balancing of the energy budget on day t by using lake trout energy density on day $t + 1$); the model was applied to each combination of tank and test period. The solid line represents the regression line fitted to the points; the dashed line represents the line of 1:1 correspondence between predictions and observations.

of weight at the end of a test period for both activity levels (Table 2). However, regression analysis did not indicate a significant bias in the predictions of weight at the end of a test period for either inactive or active lake trout (Table 2; Figure 3).

When algorithm 2 was used to balance the energy budget, bioenergetics model predictions of lake trout weight at the end of a monthly test period were unbiased for inactive lake trout and were slightly biased for active lake trout. According to the paired t-test results, the model predictions of weight at the end of a test period were not significantly biased for inactive lake trout (Table 2); regression analysis also showed no significant bias in model predictions of weight for inactive lake trout (Table 2; Figure 4). For active lake trout, the paired t-test results indicated that the bioenergetics model significantly underestimated weight at the end of a test period (Table 2). However, regression analysis showed no significant bias in the predictions of weight

for active lake trout (Table 2; Figure 4). Overall, bioenergetics model predictions of weight at the end of a test period were more accurate when using algorithm 2 than when using algorithm 1 (Figures 3, 4).

For bioenergetics model predictions of cumulative consumption over the 135-d experiment, algorithm 2 yielded significantly more accurate predictions than algorithm 1 (two-way ANOVA: $F = 51.80$; df = 1, 12; $P < 0.0001$). Activity did not have a significant effect on bioenergetics model accuracy ($F = 1.00$; df = 1, 12; $P = 0.3381$), and the interaction between activity and energy budget balancing algorithm was not significant ($F = 2.37$; df = 1, 12; $P = 0.1494$). When algorithm 1 was used, the bioenergetics model predictions of cumulative consumption over the 135-d experiment were 13–22% lower than the observed cumulative consumption (Table 1). When algorithm 2 was used, the predictions of cumulative consumption were within 5% of

observed values for inactive lake trout and were 1–15% higher than observed values for active lake trout (Table 1).

With regard to bioenergetics model predictions of cumulative growth in weight over the 135-d experiment, algorithm 2 yielded significantly more accurate predictions than algorithm 1 (two-way ANOVA: $F = 39.59$; df = 1, 12; $P < 0.0001$). Activity did not have a significant effect on bioenergetics model accuracy ($F = 2.24$; df = 1, 12; $P = 0.1606$), and the interaction between activity and energy budget balancing algorithm was not significant ($F = 0.36$; df = 1, 12; $P = 0.5588$). When algorithm 1 was used, bioenergetics model predictions of final weight were between 5% and 13% higher than observed final weight (Table 1). When algorithm 2 was used, the bioenergetics model's predictions of final weight were within 3% of observed final weight for inactive lake trout and were 1–8% lower than observed final weight for active lake trout (Table 1).

DISCUSSION

Our results clearly show that algorithm 2 outperforms algorithm 1 in terms of the accuracy of consumption and growth predictions from the bioenergetics model. Monthly consumption was significantly underestimated for both inactive and active lake trout when algorithm 1 was used. In contrast, use of algorithm 2 resulted in no detectable bias in predictions of monthly consumption by inactive lake trout and yielded only a slight overestimation of monthly consumption by active lake trout. Our paired t-test results also indicated significant overestimation of monthly growth for both inactive and active lake trout when algorithm 1 was used, whereas predictions of monthly growth based on algorithm 2 exhibited no significant bias for inactive lake trout. Moreover, for cumulative consumption over the course of the 135-d experiment, the predictions based on algorithm 2 were significantly more accurate than those based on algorithm 1. Predictions of growth in weight over the entire experiment were also significantly more accurate when algorithm 2 was used than when algorithm 1 was used. The superior performance of algorithm 2 can be attributed to its accurate balancing of the fish's energy budget, whereas use of algorithm 1 does not lead to an accurate balancing of the energy budget unless the fish's energy density remains constant over time. Stewart et al. (1983) used the energy density of lake trout on day $t + 1$ in balancing the energy budget of the lake trout on day t, and this same algorithm 2 approach was also used by Stewart (1980) in developing the bioenergetics models for Chinook salmon and coho salmon *O. kisutch*.

The slight bias in bioenergetics model predictions of consumption and growth for active lake trout based on algorithm 2 may be due to energy savings accrued from swimming in groups compared with individual swimming. The lake trout bioenergetics model developed by Stewart et al. (1983) was primarily based on respiration rate measurements of a single lake trout swimming in a respirometer tunnel. However, for certain fish species and at certain ranges of swimming speed, the average respira-

tion rate for a school of fish swimming at a given speed may be lower than the respiration rate of a single fish swimming at that same speed (Blake 2004; Liao 2007). In these cases, swimming in a group at a certain speed affords a lower amount of energy expenditure per fish than the energy expended by a single fish swimming at the same speed in a respirometer tunnel. Consequently, if the active lake trout were saving energy by swimming in a group in our laboratory tanks, then the bioenergetics model would be expected to overestimate consumption by these fish.

Based on our laboratory results, the most plausible explanation for bioenergetics models' underestimation of food consumption when fish feed at a relatively high rate is that the fish's energy density is not taken into account with a sufficient amount of accuracy. Although lake trout were fed ad libitum in our study, bioenergetics model performance was relatively good when algorithm 2 was used to balance the energy budget, whereas bioenergetics model predictions of consumption were biased conspicuously low under algorithm 1. Activity did not have a significant effect on bioenergetics model performance. Therefore, our results provided no evidence that the resting metabolic rate was higher for inactive lake trout than for active lake trout. Consequently, the underestimation of consumption for lake trout feeding at a high rate is probably not attributable to an elevation in the resting metabolic rate of inactive fish compared with active fish. In addition, our results suggest that the components of the lake trout bioenergetics model developed by Stewart et al. (1983) were accurate predictors of egestion, excretion, and SDA, as food consumption did not appear to be underestimated when algorithm 2 was used to balance the energy budget. Of course, laboratory experimentation to specifically quantify resting metabolic rate, egestion, excretion, and SDA will be needed to confirm that these effects were not responsible for the underestimation of consumption at high feeding rates.

Results from our laboratory experiment highlight the importance of properly accounting for changes in fish energy density over time when balancing the fish's daily energy budget. Relatively low feeding rates may lead to a decrease in fish energy density over time, whereas relatively high feeding rates can lead to an increase in fish energy density over time (Madenjian and O'Connor 1999). Use of algorithm 1 will result in (1) the overestimation of food consumption by a fish when that fish's energy density decreases over time and (2) the underestimation of food consumption when the fish's energy density increases over time. The degree of bias in predictions of food consumption increased with increasing magnitude of the rate of change in fish energy density over time. For example, of the eight tanks in our experiment, tank 6 had the smallest relative difference between estimates of cumulative (135-d) consumption based on the two algorithms; the estimates were 553 g for algorithm 1 and 654 g for algorithm 2, and the relative difference was about 15% (using the algorithm 2 consumption estimate as the reference estimate). Coincidentally, the lowest rate of change in lake trout energy density over the 135-d experiment was for tank 6, in which energy density increased at approximately 5 J·g^{-1}·d^{-1}.

The greatest relative difference in estimates of cumulative consumption between the two algorithms was for tank 3, with the algorithm 1 consumption estimate being 30% lower than the algorithm 2 estimate. Tank 3 also demonstrated the greatest rate of change in lake trout energy density (increasing at 21 $J \cdot g^{-1} \cdot d^{-1}$) over the entire experiment. Using equations 1 and 2 and assuming that the consumption rate is directly proportional to the estimated weight on day $t + 1$, the ratio of cumulative consumption based on algorithm 1 to that based on algorithm 2 can be approximated by Δ^n, where Δ is the average daily proportional change in fish energy density and n is the number of days in the experiment. Although this is a rough approximation because departures from the assumption can sometimes be substantial, Δ^n may still be useful in gauging the degree of bias imparted by the use of algorithm 1. As previously mentioned, algorithms 1 and 2 will yield identical estimates of consumption and growth when the energy density of the fish is constant over time.

Several examples of fish in lakes increasing their energy density at rates exceeding 5 $J \cdot g^{-1} \cdot d^{-1}$ can be gleaned from the literature; therefore, our laboratory results have applicability to the field. Juvenile lake trout and juvenile Chinook salmon from Lake Michigan typically increased their energy density at rates between 5 and 10 $J \cdot g^{-1} \cdot d^{-1}$ during the growing season (Stewart et al. 1983; Stewart and Ibarra 1991). Adult alewives in Lake Michigan increased their energy density at rates exceeding 30 $J \cdot g^{-1} \cdot d^{-1}$ between August and November (Stewart and Binkowski 1986; Madenjian et al. 2006). It should be kept in mind that in many fish populations, the energy density of the adult fish does not change appreciably as the fish continues to grow (Hanson et al. 1997; Madenjian et al. 2000). In these cases, algorithms 1 and 2 would produce very similar estimates of food consumption. Nonetheless, in some field applications, the two algorithms would yield substantially different estimates of consumption.

Our study illustrates the importance of small details in the algorithm used to balance the fish's energy budget as related to the assessment of fish bioenergetics model accuracy. Evaluation of fish bioenergetics models has been actively pursued during the past 15 years or so (Bajer et al. 2004; Trudel and Rasmussen 2006; Lantry et al. 2008). In laboratory evaluations, fish are typically fed at a variety of rates (including ad libitum) to judge model performance over a broad range of feeding rates. One pattern that has emerged from the set of evaluations to date is that fish bioenergetics models underestimate food consumption when fish feed at a relatively high rate, and this underestimation has been blamed on the models being developed with insufficient data to adequately capture all components of the fish's energy budget at a high level of food intake. Our results indicate that fish bioenergetics models can perform very well at high feeding rates provided that the changes in fish energy density over time are properly taken into account. Our colleagues at the University of Michigan (Yu-Chun Kao and others) have revised the computer code of the bioenergetics model software developed by Hanson

et al. (1997) so that the model predictions are dependent on algorithm 2 rather than on algorithm 1. Plans are being made to make the revised software package available at the website of the Center for Limnology, University of Wisconsin, Madison (limnology.wisc.edu; P. Hanson, personal communication). For future fish bioenergetics model evaluations, we recommend that researchers accurately account for changes in fish energy density over time.

ACKNOWLEDGMENTS

REFERENCES

Bajer, P. G., G. W. Whitledge, and R. S. Hayward. 2004. Widespread consumption-dependent systematic error in fish bioenergetics models and its implications. Canadian Journal of Fisheries and Aquatic Sciences 61:2158–2167.

Bajer, P. G., G. W. Whitledge, R. S. Hayward, and R. D. Zweifel. 2003. Laboratory evaluation of two bioenergetics models applied to yellow perch: identification of a major source of systematic error. Journal of Fish Biology 62:436–454.

Bence, J. R., and K. D. Smith. 1999. An overview of recreational fisheries of the Great Lakes. Pages 259–306 in W. W. Taylor and C. P. Ferreri, editors. Great Lakes fisheries policy and management: a binational perspective. Michigan State University Press, East Lansing.

Bergstedt, R. A., R. L. Argyle, J. G. Seelye, K. T. Scribner, and G. L. Curtis. 2003. In situ determination of the annual thermal habitat use by lake trout (*Salvelinus namaycush*) in Lake Huron. Journal of Great Lakes Research 29(Supplement 1):347–361.

Blake, R. W. 2004. Fish functional design and swimming performance. Journal of Fish Biology 65:1193–1222.

Bunnell, D. B., T. B. Johnson, and C. T. Knight. 2005. The impact of introduced round gobies (*Neogobius melanostomus*) on phosphorus cycling in central Lake Erie. Canadian Journal of Fisheries and Aquatic Sciences 62:15–29.

Chipps, S. R., and D. H. Wahl. 2004. Development and evaluation of a western mosquitofish bioenergetics model. Transactions of the American Fisheries Society 133:1150–1162.

Christiansen, J. S., and M. Jobling. 1990. The behaviour and the relationship between food intake and growth of juvenile Arctic charr, *Salvelinus alpinus* L., subjected to sustained exercise. Canadian Journal of Zoology 68:2185–2191.

Claramunt, R. M., T. L. Kolb, D. F. Clapp, D. B. Hayes, J. L. Dexter Jr., and D. M. Warner. 2009. Effects of increasing Chinook salmon bag limits

on alewife abundance: implications for Lake Michigan management goals. North American Journal of Fisheries Management 29:829–842.

Hansen, M. J., D. Boisclair, S. B. Brandt, S. W. Hewett, J. F. Kitchell, M. C. Lucas, and J. J. Ney. 1993. Applications of bioenergetics models to fish ecology and management: where do we go from here? Transactions of the American Fisheries Society 122:1019–1030.

Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish bioenergetics 3.0. University of Wisconsin, Sea Grant Institute, Technical Report WIS-CU-T-97-001, Madison.

Hayward, R. S., and F. J. Margraf. 1987. Eutrophication effects on prey size and food available to yellow perch in Lake Erie. Transactions of the American Fisheries Society 116:210–223.

Hewett, S. W., and B. L. Johnson. 1987. A generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin, Sea Grant Institute, Technical Report WIS-CG-87-245, Madison.

Kraft, C. E. 1993. Phosphorus regeneration by Lake Michigan alewives in the mid-1970s. Transactions of the American Fisheries Society 122:749–755.

Lantry, B. F., L. G. Rudstam, J. L. Forney, A. J. VanDeValk, E. L. Mills, D. J. Stewart, and J. V. Adams. 2008. Comparisons between consumption estimates from bioenergetics simulations and field measurements for walleyes from Oneida Lake, New York. Transactions of the American Fisheries Society 137:1406–1421.

Liao, J. C. 2007. A review of fish swimming mechanics and behaviour in altered flows. Philosophical Transactions of the Royal Society of London B 362:1973–1993.

Madenjian, C. P. 2011. Bioenergetics in ecosystems. Pages 1675–1680 in A. P. Farrell, editor. Encyclopedia of fish physiology: from genome to environment. Elsevier, Oxford, UK.

Madenjian, C. P., T. J. DeSorcie, and R. M. Stedman. 1998. Ontogenic and spatial patterns in diet and growth of lake trout in Lake Michigan. Transactions of the American Fisheries Society 127:236–252.

Madenjian, C. P., R. F. Elliott, T. J. DeSorcie, R. M. Stedman, D. V. O'Connor, and D. V. Rottiers. 2000. Lipid concentrations in Lake Michigan fishes: seasonal, spatial, ontogenetic, and long-term trends. Journal of Great Lakes Research 26:427–444.

Madenjian, C. P., and D. V. O'Connor. 1999. Laboratory evaluation of a lake trout bioenergetics model. Transactions of the American Fisheries Society 128:802–814.

Madenjian, C. P., S. A. Pothoven, J. M. Dettmers, and J. D. Holuszko. 2006. Changes in seasonal energy dynamics of alewife (*Alosa pseudoharengus*) in Lake Michigan after invasion of dreissenid mussels. Canadian Journal of Fisheries and Aquatic Sciences 63:891–902.

Neter, J., W. Wasserman, and M. H. Kutner. 1983. Applied linear statistical models. Irwin, Homewood, Illinois.

Ney, J. J. 1993. Bioenergetics modeling today: growing pains on the cutting edge. Transactions of the American Fisheries Society 122:736–748.

Stewart, D. J. 1980. Salmonid predators and their forage base in Lake Michigan: a bioenergetics-modeling synthesis. Doctoral dissertation. University of Wisconsin, Madison.

Stewart, D. J., and F. P. Binkowski. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: an energetics-modeling synthesis. Transactions of the American Fisheries Society 115:643–661.

Stewart, D. J., and M. Ibarra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978–88. Canadian Journal of Fisheries and Aquatic Sciences 48:909–922.

Stewart, D. J., J. F. Kitchell, and L. B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. Transactions of the American Fisheries Society 110:751–763.

Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsall. 1983. An energetics model for lake trout, *Salvelinus namaycush:* application to the Lake Michigan population. Canadian Journal of Fisheries and Aquatic Sciences 40:681–698.

Stow, C. A., S. R. Carpenter, C. P. Madenjian, L. A. Eby, and L. J. Jackson. 1995. Fisheries management to reduce contaminant consumption. BioScience 45:752–758.

Trudel, M., and J. B. Rasmussen. 2006. Bioenergetics and mercury dynamics in fish: a modelling perspective. Canadian Journal of Fisheries and Aquatic Sciences 63:1890–1902.

Weininger, D. 1978. Accumulation of PCBs by lake trout in Lake Michigan. Doctoral dissertation. University of Wisconsin, Madison.